

MORPHOLOGICAL AND PALEOBOTANICAL STUDIES
OF THE NYSSACEAE, II
THE FOSSIL RECORD

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AN EARLIER PAPER by the first author (Eyde, 1963) dealt with the distribution and the distinguishing characteristics of modern species of Nyssaceae and placed special emphasis on the comparative morphology of nyssaceous fruits. In the present paper, we shall take up the fossil record of the family, applying critical comments based on our studies of modern Nyssaceae whenever possible. Although in our own research we have been primarily concerned with structural features of the fruits, we have also included here a review of reports of other fossil remains — leaves, pollen, and wood — that have appeared in recent years. It is hoped that the present work will serve as a useful supplement to Kirchheimer's detailed monograph (1938) on fossil Nyssaceae.

Convincing nyssaceous fossils are not presently known from horizons below the Tertiary. The Jurassic "pollen" designated as "cf. *Nyssa*" by Reissinger (1950, Pl. XIII, figs. 11 a & b) is probably a tetrad of spores; in any case, the comparison with *Nyssa* cannot be taken seriously. Cretaceous leaf impressions that were assigned to *Nyssa* in some of the older works (Kirchheimer, 1938, pp. 119–123) are mostly poorly preserved specimens, and in view of the lack of striking identifying features in the leaves of modern *Nyssa*, these fossils can hardly be considered as evidence for the occurrence of the genus. The same comment may be made regarding a single incomplete leaf impression from the Cretaceous of Texas described by MacNeal (1958) as *N. woodbinensis*. Dorf (1942, pp. 29 & 78) compared the Cretaceous "seeds" *Carpites walcottii* with *Nyssa aquatica*. Judging from Dorf's illustrations (Pl. 19, figs. 1 & 2), however, the resemblance is very remote. *Carpites walcottii* apparently lacks a germination valve, and the apical projections found on this fossil have no counterpart in bona fide remains of *Nyssa*. Recently Samylina (1961) compared some ribbed fruits (?) from the Lower Cretaceous of the Maritime Territory, U. S. S. R., with fruits of *Nyssa*, applying the names *Nyssidium orientale* and *Nyssidium* sp. to her fossils. Samylina's comparison is based on a fancied resemblance between the nyssaceous germination valve and an unsculptured region at one end of each *Nyssidium* specimen. In fruits of Nyssaceae, however, major external ridges and grooves pass over the entire stone, including the germination valve. The fact remains that we have no knowledge of the Mesozoic antecedents of *Nyssa*.

TERTIARY LEAVES

All of the supposedly nyssaceous leaf remains found in Tertiary deposits have been compared to *Nyssa* with one exception: Johnson (1937) described several impressions taken from Eocene beds of the Isle of Mull as *Davidioidea hebridica* because of their resemblance to leaves of modern *Davidia*. The first author recently saw some of these fossils on display in the British Museum (Nat. Hist.), London, and will confirm the general similarity to *Davidia*. However, as Kirchheimer noted (1938, p. 117), comparable leaves are also found in *Tilia*; therefore, these fragments can hardly be taken as proof that an ancient davidiod tree once grew in Scotland.

The name *Nyssa* has been applied to numerous Tertiary leaf impressions collected in the northern hemisphere during the past hundred years. In many cases the impressions are incomplete and details are not preserved. Even when preservation is good, it is difficult to establish the occurrence of the genus from the leaves alone, for most *Nyssa* foliage is without conspicuous identifying features. Kirchheimer has observed that leaves and leaflets resembling entire-margined leaves of *Nyssa* may be found in genera of Annonaceae, Moraceae, Juglandaceae, Fagaceae, Magnoliaceae, Lauraceae, Sapindaceae, Ebenaceae and Apocynaceae (1938, p. 78). On the other hand, some of the reports of *Nyssa* currently appearing in paleobotanical literature not only are based on well-preserved leaf impressions but also are supported by associated nyssoid pollen or fruits and by the remains of other plants that would be found today associated in a *Nyssa-Taxodium* swamp.

Kirchheimer catalogued very meticulously the fossil leaves attributed to *Nyssa* in literature published prior to 1938; therefore, we shall mention only those that have been reported since that date. The name *N. europaea*, originally published by Unger in 1845, has been applied during the past decade to leaf remains from the Miocene of Poland (Kownas, 1955) and to Pliocene impressions from Georgian S. S. R. (Kolakovskiy, 1957) and from the Vienna Basin (Berger, 1952). A new name, *N. rottensis*, was applied by Weyland (1941) to leaves collected in Oligocene beds of Germany; subsequently this name was treated as a synonym of *N. europaea* Ung. by Kownas (1955). Other new names that have been assigned to supposedly nyssoid leaf impressions by European authors are *N. zaisanica* Grubov (*in* Krishtofovich, 1956), based on Oligocene material collected near Lake Zaysan in Kazakhstan, and *N. hungarica* Andreánszky (1959), based on a specimen from the Sarmatian beds of northern Hungary. Andreánszky's fossil has been compared with the foliage of modern *N. aquatica* because of its size and its coarsely serrated margin. Johnson (1941) used the name *N. elliptica* in describing a leaf imprint from presumably Oligocene sediments of County Tyrone, Northern Ireland, but the very brief description is unaccompanied by an illustration; consequently, Johnson's name has no validity under the International Code of Botanical Nomenclature. Krishtofovich and Baykovskaya referred to a leaf imprint

(1951, Pl. VI, fig. 2) found in Miocene deposits of the Donets Basin simply as "*Nyssa* sp.", and Pantić (1956) listed *Nyssa* as a constituent of a lower Miocene leaf-florule in Yugoslavia.

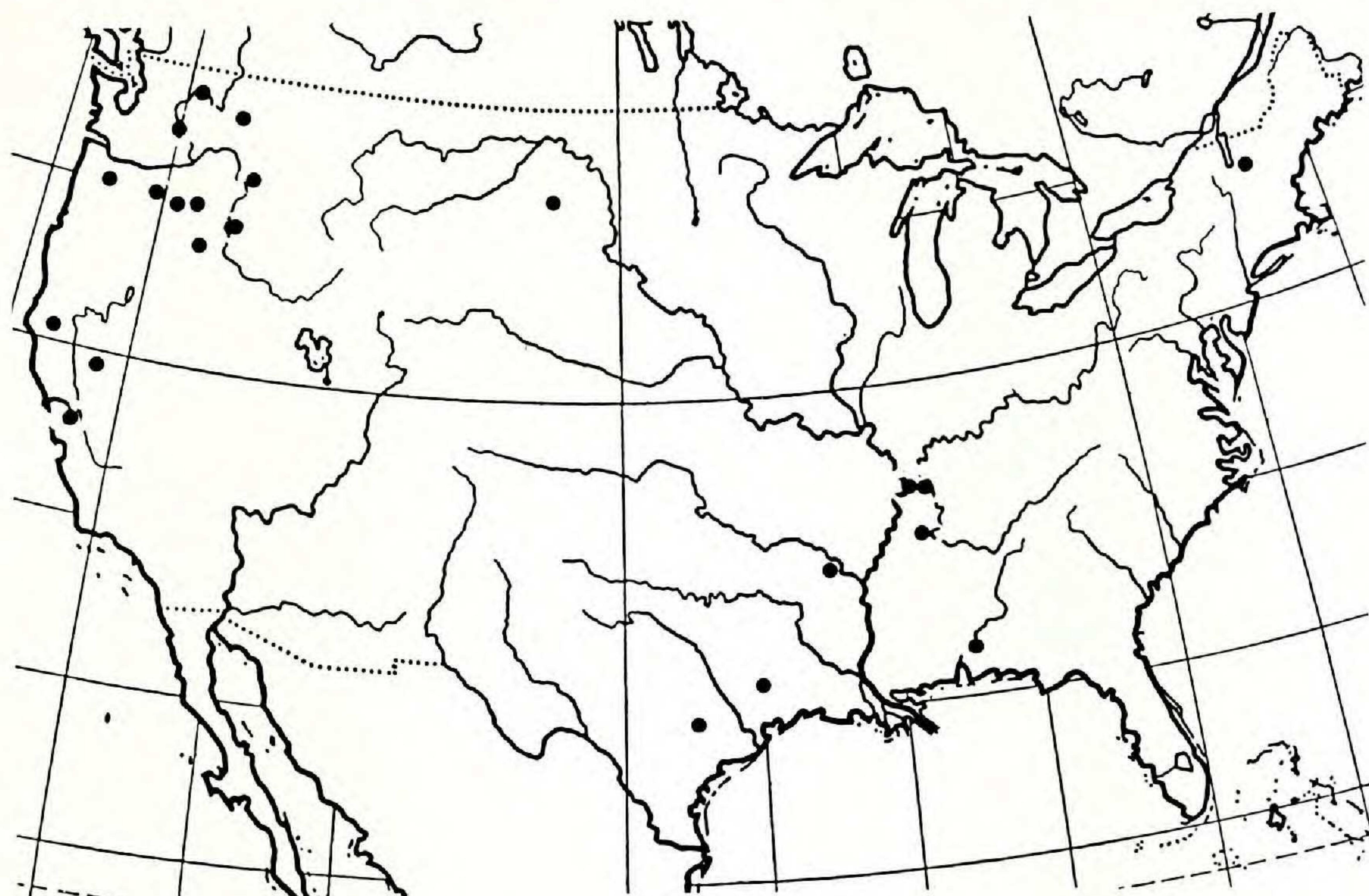
Probably the most reliable of all the European reports is that of Kräusel and Weyland (1954), who based their identification on a microscopic comparison between epidermal cells of modern *Nyssa* leaves and leaves obtained from Oligocene beds of East Germany.

Leaf impressions that are presumably referable to *Nyssa* have been reported frequently from Tertiary deposits of the western United States. Chaney and Axelrod (1959) simplified the treatment of these remains by combining many specimens from different horizons and localities into two fossil species, *N. copeana* (Lesq.) Chaney & Axelrod and *N. hesperia* Berry. The first of these species includes leaves formerly referred to *N. elaeoides* Lesq. (Condit, 1944; Axelrod, 1944), *N. oregonensis* Smith (1938), and to other genera as well. The closest modern equivalent is said to be *N. sylvatica*. The name *N. hesperia* was originally applied by Berry (1931) to fruits preserved as casts in the Latah formation at Spokane, Washington. Chaney and Axelrod follow the broadened usage begun by Brown (1937b, 1946) in assigning many of the leaves previously called *N. knowltonii* to *N. hesperia*. According to these authors, the fruits resemble markedly those of modern *N. aquatica*.

We find that the similarity between *Nyssa hesperia* and *N. aquatica* has been overstated. The fossil fruits from Spokane are in fact morphologically similar to fruits of the *N. sylvatica* alliance, a point which will be taken up in another section of this paper. Admittedly, the venation of the fossil leaves figured by Brown (1937a, Pl. 62, figs. 1–3; especially fig. 3) is matched in leaves of *N. aquatica*. However, the coarse, subapical teeth that Brown took to indicate a relationship with *N. aquatica* are not comparable in position to the more basally situated teeth sometimes found on the leaf-margins of this species. (Teeth are occasionally present on leaves of *N. ogeche* and *N. sylvatica* as well, but we have never seen a leaf of any species of *Nyssa* on which the teeth were located only near the apex.)

Other American leaf impressions were described by MacGinitie (1941, p. 152) as *Nyssa californica*. These leaves were found in the Eocene Chalk Bluffs flora of California along with nyssoid fruits. MacGinitie compared the leaves with modern *N. sylvatica* and included both organs under one specific name, citing a fruit as the holotype (Pl. 40, fig. 4). More recently, Becker (1961) designated leaf impressions from the Oligocene Ruby River flora as *N. crenata*, a name originally coined by Chaney (1920). Smiley (1961, p. 177) mentions *Nyssa* as a member of the Miocene Ellensburg flora; however, his systematic treatment has not been published at the time of this writing.

Brown's posthumous work on the Paleocene flora of the Rocky Mountains and Great Plains (1962) includes the new combination *Nyssa alata* (Ward) Brown and a new species, *N. borealis*. The names are applied to fossils resembling modern leaves of *N. sylvatica* and *N. aquatica*, respectively.



MAP. 1. Reports of Tertiary Nyssaceae in North America (fruits, pollen, wood). Copyright, Rand McNally Co.

TABLE I and the distribution maps (MAPS 1-3) do not include records based only on leaf impressions, because such records are often doubtful or completely worthless. However, when leaves resembling *Nyssa* have been reported in association with nyssoid pollen or fruits, this fact has been noted in TABLE I.

TERTIARY POLLEN

The tricolporate pollen grains of modern Nyssaceae have been described by Wodehouse (1935, 1942), Erdtman (1952), and Chao (1954), and by a number of other workers who have had occasion to examine modern pollen in connection with their fossil studies. Among the latter are Ingwersen, who presented a very detailed description (1954, pp. 58-60), and Traverse (1955), who offered observations on the Asiatic nyssas, which are not included in most works. The pollen of *Camptotheca* is said to be very similar to that of *Nyssa*, and the two would not be readily separable in the fossil condition. According to Erdtman (1952), *Davida* pollen differs morphologically from the pollen of other nyssaceous species; according to Chao (1954, p. 99), however, there are no significant morphological differences between nyssoid and davidioid pollen.

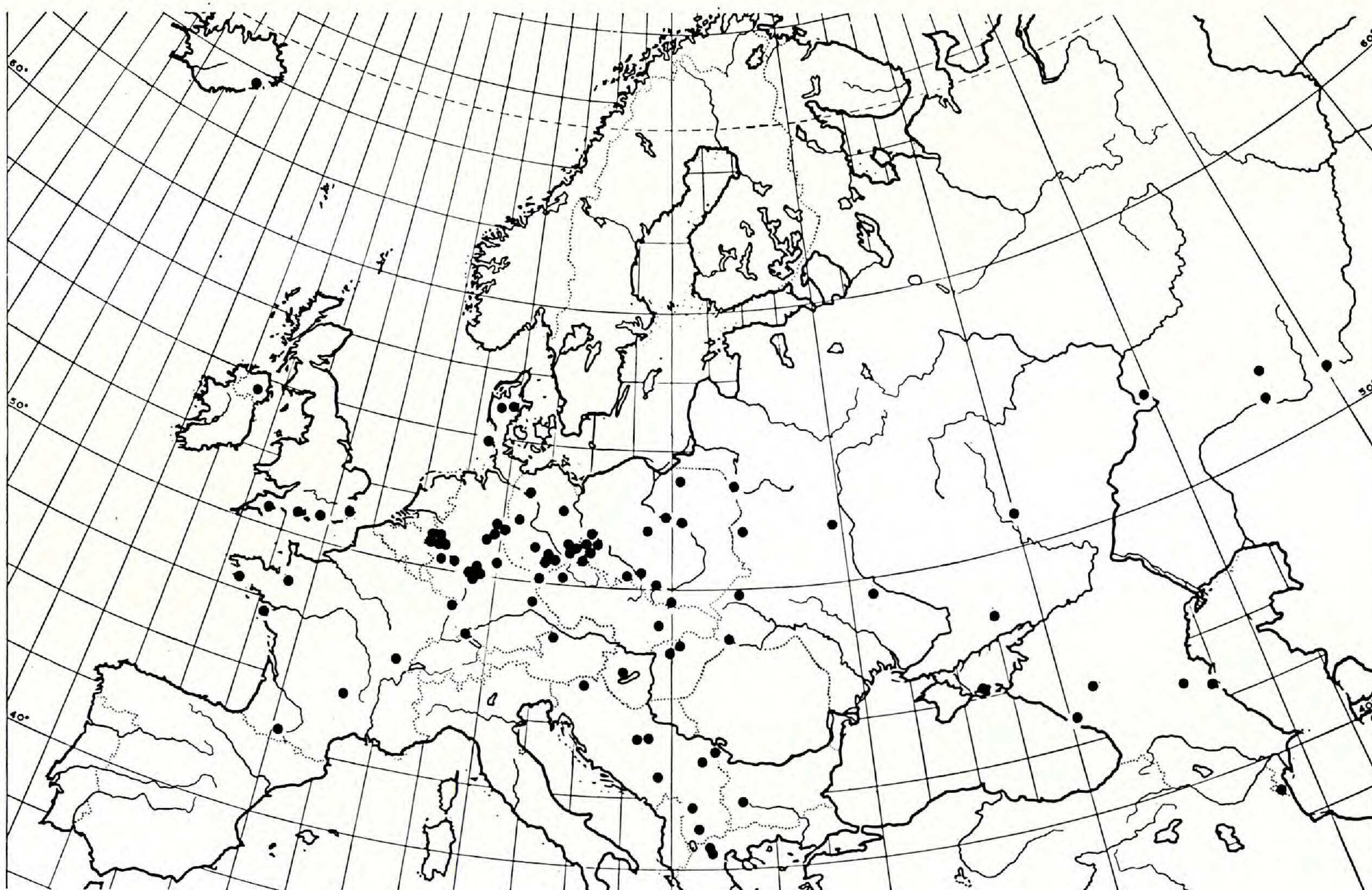
Pollen grains of modern *Nyssa sylvatica* measured by Macko (1959) were 29 μ and 31 μ in diameter; the average polar diameter obtained by Chao (1954) from this same species was 45.9 μ . Almost all of the published measurements obtained from any modern nyssaceous species would

fall between these two extremes; however, *Davidia* pollen is said to be somewhat smaller (Erdtman, 1952), and the diameter of *N. ogeche* pollen has been reported as 51 μ (Wodehouse, 1942). The latter report is of interest because large fossil forms have been reported by several authors, e.g., *Nyssa ingentipollinia* Traverse (1955), *Nyssoidites rodderensis* Thiergart (Potonié, 1960), and *Nyssa* f. *magna* (Doktorowicz-Hrebnicka, 1957a). This suggests that a careful comparative study of fossil and modern *Nyssa* pollen might enable one to infer affinities below the generic level. It should be added in passing that some of the fossil pollen that has been assigned to Nyssaceae is smaller than pollen of the modern species. Pokrovskaya (1956b, pp. 200, 201) figures grains as small as 16.5 μ in diameter.

Nomenclatural treatment of fossil pollen grains differs widely from author to author, some workers favoring a natural system, others a "half-natural" system, still others a completely artificial system. Thus, nyssoid pollen grains have been recorded as *Nyssa*, as *Nyssapollenites*, and *Nyssoidites* (Potonié, 1960), and as *Tricolporopollenites* (Thomson & Pflug, 1953). Many authors elect not to coin specific epithets for fossil pollen and simply report "*Nyssa* sp.," appending numerical subscripts (Pokrovskaya, 1956a, p. 351) or letters, etc., when the nyssoid pollen can be subdivided on the basis of size or of minor morphological features. Other authors treat the microfossils in the same manner as macroscopic remains, assigning binomials according to the International Code of Botanical Nomenclature. For instance, the names *Nyssa neshobensis*, *N. thompsoniana*, and *N. ingentipollinia* were given by Traverse (1955) to exines found in the Brandon lignite. In the system originated by Thomson and Pflug, the binomial *Tricolporopollenites kruschii* R. Pot. is applied to exines with the same morphological characteristics as modern nyssaceous pollen, and variants in size and minor features are indicated as "subspecies": *T. kruschii* subsp. *analepticus* R. Pot., *T. kruschii* subsp. *triangularis* Stanley, etc.

As a result of the rapid world-wide increase in palynological research during the past two decades, nyssaceous pollen has been collected from a great many localities in Europe, Asia, and North America and from all Tertiary horizons, Paleocene through Pliocene. Some localities have yielded only a single questionable exine, but in others (e.g., Raukopf, 1959, p. 17) the nyssoid grains constitute more than 10 per cent of the arboreal pollen.¹ Localities from which nyssaceous pollen has been recorded are listed in TABLE I. We have not attempted a critical evaluation of each report, because in many cases there is no accompanying illustration. Most of the European records are supported by associated fruit-remains, by paleoecological evidence, and by the opinions of distinguished palynologists. On the other hand, Kirchheimer (1938, p. 133) and Thomson (1954, p. 337) have mentioned the possibility of confusing the smaller nyssoid

¹ Lewis and Cocke (1929) found that the pollen of *Nyssa* reaches a maximum of 40 per cent of the total pollen a foot below the soil-surface of the Dismal Swamp, a locality where trees of *Nyssa* are very abundant today.



MAP 2. Reports of Tertiary Nyssaceae in Europe (fruits and pollen). Copyright, Rand McNally Co.

exines with pollen of Rhamnaceae and Vitaceae, and a number of authors have stated their belief that the so-called *Nyssa* pollen collected from early Tertiary beds was produced by ancient mastixioid trees as well as by nyssaceous trees (see, for instance, Thiergart, 1945, pp. 63–65).

In compiling TABLE I, we have attempted to be thorough; undoubtedly, however, some localities have been overlooked. A truly complete compilation would be very difficult in view of the great diversity of works in which palynological reports now appear. Some of these works, especially those in Slavic languages, are not obtainable even in our major libraries. Furthermore, we have not intentionally included reports based on a single pollen grain or reports regarded by their authors as questionable, with one exception: the recording of pollen resembling *Nyssa* from the early Tertiary of Kotel'nyy Island in the Arctic Ocean (Kuprianova, 1960, Pl. V, fig. 2). This locality is particularly interesting because it is by far the most northern site from which *Nyssa* has been reported in recent years. (All of the older records of Arctic *Nyssa* were based on poorly preserved leaves and misidentified fruits.) The same deposits yielded pollen of *Liquidambar*, Taxodiaceae, and other temperate plants.

TABLE I. Localities From Which Fossil Nyssaceae Have
Been Reported

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
UNITED STATES			
Harding Co., S. D.	Paleo	P	Stanley, 1960
Nevada Co., Calif. (Chalk Bluffs flora)	M Eo	Fr, L	MacGinitie, 1941
Wheeler Co., Calif. (Clarno flora)	U Eo	Fr	Scott, 1954
Trinity Co., Calif. (Weaverville flora)	M Oligo	Fr, L	MacGinitie, 1937
Vantage, Wash.	Mio	W	Prakash & Barghoorn, 1961
Spokane, Wash.	M Mio	Fr, L	Berry, 1929
Grand Coulee, Wash.	M Mio	Fr, L	Berry, 1931
Whitebird, Ida.; Washington Co., Ida.	M Mio	Fr, L	Berry, 1934
Mascall flora near Dayville, Ore.	Mio	Fr, P, L	Chaney & Axelrod, 1959; Gray, 1958
Stinking Water flora near Drewsey, Ore.	Mio	P	Gray, 1958
Blue Mt. flora near Bates, Ore.	Mio	P, L	Gray, 1958; Chaney & Axelrod, 1959

* Paleo = Paleocene; L Eo = lower Eocene; M Oligo = middle Oligocene; U Mio = upper Miocene; etc. In most cases we have simply repeated the age suggested by the cited author. Some of these stratigraphic opinions, notably Kirchheimer's (see Quitzow, 1952), have been disputed.

† Fr = fruit; P = pollen; W = wood; L = leaf.

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
UNITED STATES (continued)			
Northern Cascade Mts.,			
Ore.	Mio	P	Wolfe, 1962
San Pablo, Calif.	U Mio	Fr, L	Condit, 1938
Benton, Ark.	L Eo	P	Jones, 1960
Chester Co., Tenn.	L Eo	Fr	Berry, 1930
Puryear, Tenn.	M Eo	Fr	Berry, 1916a
Bell City, Ky.	M Eo	Fr	Berry, 1930
Hardeman Co., Tenn.	M Eo	Fr	Berry, 1930
Smithville, Tex.	M Eo	Fr	Berry, 1924
Lufkin, Tex.	M Eo	Fr	Berry, 1924
Claiborne Bluffs, Ala.	M Eo	P	Gray, 1960
Trinity Co., Tex.	Oligo	Fr	Berry, 1924, and present paper
Columbus, Ky.	Oligo	Fr	Present paper
Karnes Co., Tex.	Oligo	Fr	Present paper
Brandon, Vt.	Early Tertiary	Fr, P	Present paper; Traverse, 1955
ICELAND			
Hoffell on the Hornafjord	Mio or Plio	P	Schwarzbach & Pflug, 1957
NORTHERN IRELAND			
Lough Neagh Clays	L or M Oligo?	P	Watts, 1962
GREAT BRITAIN			
London Clay localities:			
Sheppey; Herne Bay;			
Bognor	L Eo	Fr, P	Chandler, 1961; Macko, 1961
Bournemouth Beds and			
Bagshot Beds	M Eo	Fr	Chandler, 1962
Bovey Tracey, Devon.	M Oligo	Fr	Chandler, 1957
FRANCE			
St. Tudy (Finistère)	M Eo	Fr	Reid, 1927
La Sennetièvre (L.A.)	Eo	P	Durand, 1960
Landéan (I.-et-V.)	Oligo	P	Durand, 1959
Orignac (H.-P.)	Mio	P	Sittler, 1958
Joursac & Sainte-Reine (Cantal)	Mio	P	Sittler, 1958
Allèriot (S.-et-L.)	Oldest Plio	P	Sittler, 1958
Soufflenheim (B.-R.)	U Plio	Fr	Kirchheimer, 1957
NETHERLANDS			
Heerlen	L Mio?	P	Weyland & Takahashi, 1961
Haanrade	M Mio	P	Manten, 1958
Swalmen; Reuver	Plio	Fr, P	Reid & Reid, 1915; Kirchheimer, 1957; Altehenger, 1959, p. 35

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
DENMARK			
Salten; Silkeborg	U Oligo?	Fr	Kirchheimer, 1957
Bjerregårde; Studsgård	Mio	P	Ingwersen, 1954
GERMANY			
Antweiler	Paleo & Eo	P	Thomson & Pflug, 1953
Helmstedt	Paleo & Eo	P	Thomson & Pflug, 1953
Geiseltal near Merseburg	M Eo	P	Thomson & Pflug, 1953
Messel near Darmstadt	M & U Eo	P	Thomson & Pflug, 1953
Kassel	UEo to L Oligo	P	Thomson & Pflug, 1953
Herzogenrath near Aachen	M or U Oligo	Fr	Kirchheimer, 1957
Rur Valley near Düren	M or U Oligo	Fr	Kirchheimer, 1938; Thomson, 1958
Rott near Bonn	U Oligo?	P, L	Thiergart, 1958; Weyland, 1941
Niederpleis near Siegburg	M or U Oligo	Fr	Kirchheimer, 1957
Offenbach on the Main	M or U Oligo	Fr	Kirchheimer, 1938
Sieblos (Rhön Mts.)	M Oligo	Fr	Kirchheimer, 1957
Regis near Altenburg, Saxony	Oligo	L (cuticle)	Kräusel & Weyland, 1954
Vicinity of Mittweida & Grimma, Saxony	M or U Oligo	Fr, P	Kirchheimer, 1938 & 1957; Hunger, 1952
Klettwitz near Senftenberg	M or U Oligo	Fr	Kirchheimer, 1957
Wiesa near Kamenz	M or U Oligo	Fr	Kirchheimer, 1957
Marxheim in the Lower Main region	U Oligo	P	Mürriger & Pflug, 1952
Schacht Houtgen near Krefeld	M Mio	P	Brelie, von der, 1958
Ville near Köln	Mio	Fr, P, L (cuticle)	Thomson, 1958; Neuy-Stolz, 1958; Kräusel & Weyland, 1954
Salzhausen near Nidda	U Mio	Fr	Kirchheimer, 1957
Öhningen on the Boden See	U Mio	Fr	Kirchheimer, 1955
Berlin; Malliss in Mecklenburg; Jahmen in the Lausitz	Mio	P	Raukopf, 1959
Haidhof near Ponholz, Bavaria	U Mio	Fr	Kirchheimer, 1938
Wackersdorf, Bavaria	Mio	P	Meyer, 1956
Icksberg near Kaldenkirchen	Reuverian	Fr	Kirchheimer, 1957
Weilerswist, North Rhine- Westphalia	Plio	P	Altehenger, 1959
Lower Main Valley: Höchst; Niederursel; Niederrad	Reuverian	Fr	Kirchheimer, 1957
Wetter Valley near Friedberg	Reuverian	Fr, P	Kirchheimer, 1957; Leischik, 1956

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
GERMANY (continued)			
Sylt, North Frisian Is.	Reuverian Plio	P	Weyl, Rein, & Teichmüller, 1955
Brunswick: Wallensen; Willershausen; Solling near Uslar			
	Plio	P	Altehenger, 1959
AUSTRIA			
Ampflwang in Hausruck	L Plio?	P	Meyer, 1956
POLAND			
Zittau Valley	L Mio	Fr	Czeczott, Zaléwska, & Skirgiello, 1959
Miroslawice Gorne	L Mio	P	Doktorowicz-Hrebnicka, 1957b
Kłodnica Valley near Gliwice	L Mio	P	Macko, 1957
Konin on the Warta	Mio	P	Kremp, 1949
Dobrzyń on the Vistula	Mio	Fr, L	Kownas, 1955
Nowa Wies near Opole; Łączi near Nysa; Węgliniec Basin	Mio	P	Macko, 1959
Sites near Nielona Góra (Grünberg), Głogów, and Bolesławiec (Bunzlau), all in Lower Silesia	U Mio	Fr	Kirchheimer, 1957
Poznań clays: vicinity of Olsztyn and NW of Warsaw	L or M Plio	P	Doktorowicz-Hrebnicka, 1957a
Krościenko; Huba; Mizerna	Reuverian Plio	Fr, P	Szafer, 1946, 1954
HUNGARY			
Halimba	L Eo	P	Kedves, 1961
Petöfi-bánya near Hatvan	Plio	P	Nagy, 1959
Eger	Helvetian Mio	Fr	Zeller-Igali, 1955
CZECHOSLOVAKIA			
Vrsovice near Louny (Laun)	L Mio	Fr	Kirchheimer, 1957
Handlová	U Mio	P	Pacltová, 1958
Vonšov (Fonsau) near Cheb	Plio	P	Rudolph, 1935
YUGOSLAVIA			
Ugljevik in NE Bosnia	Late Oligo-early Mio	P	Weyland, Pflug, & Pantić, 1958
Pljevlja in Montenegro	M Mio	P	Weyland, Pflug, & Pantić, 1958

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
YUGOSLAVIA (continued)			
Despotovac in Serbia	U Mio	P	Weyland, Pflug, & Pantić, 1958
Jabukovac in Serbia	Sarmatian Mio	Fr	Pantić, 1957
Kreka near Tuzla	Pontian (Mio-Plio)	P	Weyland, Pflug, & Pantić, 1958
Oslovey Mine near Kičovo	Plio	P	Pantić & Nicolić, 1956
Velenje in Slovenia	Reuverian Plio	P	Weyland, Pflug, & Pantić, 1958
GREECE			
Vévi	Plio	P	Weyland, Pflug, & Pantić, 1958
Ptolemaïs	Plio	P	Weyland, Pflug, & Müller, 1960
BULGARIA			
Dospey near Samokov	Oligo	Fr	Palamarev, 1961
U.S.S.R.			
White Russia:			
northwestern part	U Eo	P	Manykin, 1958b
White Russia: southern part	Oligo-Mio	P	Manykin, 1958a
L'vov, Ukrainian SSR	Tortonian Mio	P	Shchekina, 1956, 1957
Vinogradov, Trans-Carpathian Ukraine	Tortonian Mio	P	Shchekina, 1958a
Cherkassy Region, Ukrainian SSR	M Eo	P	Shchekina, 1958b
Environs of Kiev	Poltavian Mio	P	Shchekina, 1962
Novotroitskoye near Volnovakha, Ukrainian SSR	Oligo	P	Karlov, 1956
Kerch Peninsula, Crimea	Plio	P	Maslova, 1961
Voronezh Region	Early Tertiary	P	Zaklinskaya, 1953a
Solenovskaya near the Lower Don	Mio	P	Pokrovskaya, 1956b
Cherkessk on the Kuban	Oligo	P	Kozyar, 1957
Dub River, western Caucasus	Plio	Fr, P	Kolakovskiy, 1958
Karabudakhent; other localities in Dagestan & Checheno-Ingush	Oligo & Mio	P	Grossgeym & Gladkova, 1951; Gladkova, 1953; Pokrovskaya, 1956a, 1956b
Talysh Mts., Azerbaijan SSR	Oligo-Mio	P	Dzhabarov & Kasumova, 1961
Zhilgi Mts., Volga Valley	M Plio	P	Grishchenko & Glushchenko, 1956

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
U.S.S.R. (continued)			
Southern Urals near Yumaguzino & Chernyy	Oligo	P	Pokrovskaya, 1956b
Otrog			
Urals: Kolchin near Bredy; Bilimbay near Chelyabinsk	Mio	P	Pokrovskaya, 1956a
Turgay Depression; Zhilanchik Basin; NW Kazakhstan & Kurgan Region	Eo, Oligo, & Mio	P	Pokrovskaya, 1954, 1956a, 1956b; Abuzyarova, 1955, 1958; Boytsova & Pokrovskaya, 1954; Kornilova, 1955; Zaklinskaya, 1955; Rzhankova, 1956
Pavlodar on the Irtysh & vicinity	Eo, Oligo, & Mio	P	Zaklinskaya, 1953b
Ashutas Mt. near Lake Zaysan	Oligo	Fr, P, L	Krishtofovich, 1956; Il'inskaya, 1957; Rzhankova, 1958
Antropovo on the Tavda Uvat; Lar'yak; other sites on the W. Siberian Lowland	Oligo	Fr	Dorofeyev, 1961
Tara on the Irtysh	L Oligo	P	Pokrovskaya, 1956b
	Mio	Fr	Krishtofovich & Borsuk, 1939
Tebisskaya Station near Barabinsk	Mio	P	Pokrovskaya, 1956a
Rezhenka near Tomsk	Oligo	Fr	Dorofeyev, 1958
Kireyev Ravine near Tomsk	Early Mio?	Fr	Dorofeyev, 1960b
Zaobsky Ravine near Tomsk	Mio?	Fr	Kolesnikova, 1961
Dunayevsky Ravine on the Tym	Oligo	Fr	Dorofeyev, 1960a
Kotel'nyy Island	Paleo?	P	Kuprianova, 1960
Lower Aldan R. near Ust' Tatta	?	P	Khoreva & Giterman, 1961
Smirnovka on the Amur	Oligo	P	Fin'ko & Zaklinskaya, 1958
Maykhe R.; Suputinka R.; other sites in southern Maritime Territory	Oligo & Mio	P	Pokrovskaya, 1956a, 1956b; Sedova, 1957

TABLE I. (*Continued*)

LOCALITY	AGE *	KIND OF FOSSIL †	REFERENCE
JAPAN			
Kushiro coalfield, Hokkaidō	Mio	P	Okazaki, 1952
Ombetsu R., Hokkaidō	?	W	Mädel, 1959
Aomori Pref., Honshū	Plio	P	Sohma, 1958c
Sendai, Honshū	Mio & Plio	P	Sohma, 1956, 1957a, 19- 57b, 1958a
Nagoya, Honshū	Plio	P	Sohma, 1958b
NE Shikoku	U Plio	P	Sohma, 1960
Nahari, Shikoku	Plio	P	Jimbō, 1958
Ca. 25 sites in northern & central Honshū; one site in Kyūshū	Plio	Fr	Miki, 1956

TERTIARY WOODS

Fossil woods of Nyssaceae are extremely rare. Apparently none were described in the scientific literature until Beck (1945) reported a collection of two dozen specimens gathered in Idaho, Oregon, and central Washington. Beck did not attempt a formal systematic and descriptive treatment of his woods, but he did section the fossils, and he compared them with sections of woods of three modern *Nyssa* species — *N. sylvatica*, *N. aquatica*, and *N. ogeche*. He found that all of the modern woods used for reference could be matched by one or more of his fossils. Beck concluded that we have the choice of "one extremely variable Miocene species or as many or more species as represented in eastern America today."

Subsequently, Prakash and Barghoorn (1961) discovered a single specimen of silicified *Nyssa* wood among material collected from the Miocene Columbia Basalts near Vantage, Washington, the same area from which Beck obtained most of his *Nyssa* fossils. This wood was described in detail and designated as a new fossil species, *N. eydei*. The authors stated (p. 354) that "a survey of the structural features of the fossil indicates that the nearest affinity of the fossil is with *Nyssa ogeche*."

The comparison of *Nyssa eydei* with modern *N. ogeche* was stated rather emphatically, because the imperforate tracheary elements of the fossil wood have exceptionally thin walls and large lumina, features that are characteristic of *N. ogeche* specimens in the reference collection of the Arnold Arboretum. While preparing the present paper, however, we had occasion to re-examine the reference slides in association with Dr. Prakash, and we found that this collection also contains some specimens of *N. aquatica* wood in which the fibers have thin walls and large lumina. Possibly these thinner-walled specimens of *N. aquatica* were taken from the lower portions of trees: Penfound (1934) reported that the wall thickness of all wood components in trees of this species is less at the base of the trunk than at higher levels. (It is well-known that the spongy root-wood was formerly

used to make surgeon's tents. See, for instance, *Merck's 1907 Index*, p. 450.) Gradation in wall thickness in wood of *N. aquatica* is apparently related to the swamp habitat, and it seems not unlikely that a similar gradation would also be found in stems of other aquatic nyssas. At any rate, thin-walled structure is not confined to wood of *N. ogeche*; therefore, the presence of this character in the fossil *N. eydei* cannot be taken as proof that *N. ogeche* is its nearest living equivalent.²

So far there has been only one other nyssaceous wood described in the paleobotanical literature. The specimen was found as a pebble in the Ombetsu River near Kushiro, Japan, and its stratigraphic source is not known. Mädel (1959) described the fine structure of this fossil and assigned it to *Nyssoxylon*, a form-genus created to include fossil woods showing features in common with modern *Nyssa* and *Davida*. The Japanese fossil was named *Nyssoxylon japonicum* Mädel and this species was designated as the type of the new genus.

Mention of a fossil *Nyssa* wood is made in the unpublished doctoral dissertation of Dukes (1961). The exact source of the silicified specimen that Dukes believes to be a *Nyssa* remnant is unknown; the wood was acquired from a collector in Louisiana, and it may be of Wilcox (lower Eocene) age.

TERTIARY FRUITS

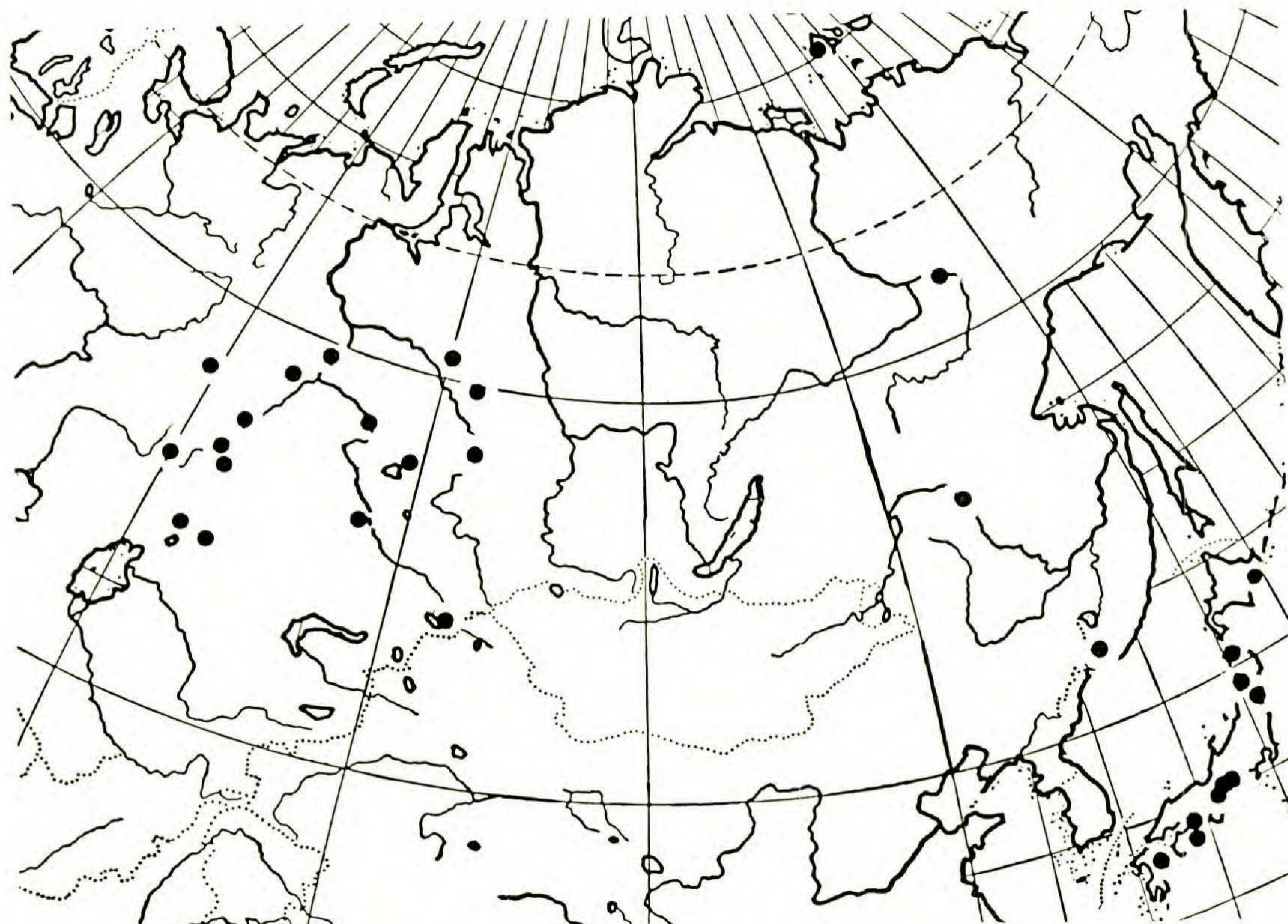
Paleobotanists of the 19th century frequently compared any longitudinally ridged or striated fruit with *Nyssa*. As a result, a map presented by Berry (1923, p. 245), which purported to show the ancient distribution of *Nyssa*, contained a number of Arctic localities. These represented, at least in part, records of "*Nyssidium*" fruits, which Heer (1870) had erroneously compared with modern *Nyssa*. Subsequently, Brown (1939) transferred Heer's *Nyssidium* species, along with leaves formerly known as *Nyssa arctica* Heer and *Nyssa reticulata* Heer, to *Cercidiphyllum*. The fossil fruits *Nyssa denveriana* Knowlton and *Nyssa? racemosa* Knowlton were transferred to *Cercidiphyllum* at the same time. Many of these same fossils have since been assigned to *Trochodendrocarpus* by Khrishtofovich (1958).

The characteristic germination valve of the *Nyssa* stone was discovered³

² Sudworth and Mell, in their key for distinguishing American "gumwoods," (1911, pp. 13, 14) listed thin-walled fibers as an identifying characteristic of *N. ogeche*, but later workers have not found this key to be of value. Wood anatomists of the Forest Products Research Laboratory, Great Britain, have expressed doubt that woods of American *Nyssa* species can be separated (Brazier and Franklin, 1961, p. 30), and Dr. B. F. Kukachka, wood anatomist of the U. S. Forest Products Laboratory, has written, "So far as I am concerned, the normal stem wood of the various species is so similar as to preclude the possibility of specific determination with any degree of certainty." (Letter to Eyde dated October 20, 1961).

³ Actually, the method of germination was known to Mark Catesby, who published the earliest botanical description of a *Nyssa* tree and to Peter Collinson, who first introduced the genus into England. The phenomenon is mentioned in a posthumous work of Catesby's (1763, p. 11) and in a letter written by Collinson to John Bartram in 1741 (Darlington, 1849, p. 147).

by C. and E. M. Reid during their paleobotanical researches (1915) and later reported by Hill (1933). The detection of this structure made possible the easy recognition of most well-preserved *Nyssa* fruits and the rejection or transfer of many fossils that had been mistakenly referred to Nyssaceae. Thus, forms previously known as *Nyssa obovata* Weber, *Nyssites* Geyler & Kinkelin, and *Pseudonyssa* Kinkelin have been placed in *Styrax* (see Kirchheimer, 1957, pp. 315, 316), and several of the "Nyssa" species found in the Bovey Tracey lignite have turned out to be *Symplocos* (Chandler, 1957).



MAP. 3. Reports of Tertiary Nyssaceae in Asia (fruits, pollen, wood).
Copyright, Rand McNally Co.

During the past 30 years, the various revisionary treatments by Chandler, Kirchheimer, and Miki have established sound taxonomic order in the European and Japanese collections of fossil *Nyssa* fruits. Since these authors have not had access to American specimens, however, the record in this hemisphere has remained in confusion. This is especially true of the abundant and excellently preserved *Nyssa* fruits of the Brandon, Vermont, brown coal deposit, for these remains had been very poorly investigated, in spite of the fact that they excited considerable botanical interest, from time to time, for more than a century.

Historical details regarding the Brandon lignite have been presented elsewhere (see Barghoorn and Spackman, 1950; Traverse, 1955) and need not be reviewed here except where the fossil *Nyssa* fruits are concerned. The first scientific paper dealing with the lignite, written by Edward Hitchcock and published in the *American Journal of Science* (1853), included 20

sketches of fossil fruits and seeds, some of them exhibiting the characteristic nyssoid germination valve. This paper was also published in 1853 as pp. 22–34 of House Document 39, Commonwealth of Massachusetts. Hitchcock presented preliminary descriptive comments on the fossils, but he assigned no names to them; instead he sent a set of specimens to Leo Lesquereux, at that time America's foremost authority on fossil plants, who published further descriptive remarks and assigned binomials. Meanwhile, Hitchcock prepared a modified version of his 1853 paper — with additional drawings — and published this in his *Report on the Geology of Vermont* (1861). Lesquereux's paper containing the names of the fossils was duplicated in the second volume of the *Report*. Nomenclaturally, this is an unusual situation: Lesquereux's names are validated by illustrations that appeared earlier in Hitchcock's paper. Moreover, both papers were presented twice in the scientific literature — first in the *American Journal of Science*, then in the *Geology of Vermont*.

Since the pioneer work of Hitchcock and Lesquereux, there has been only one attempt at a general systematic treatment of the Brandon fruit remains, that of G. H. Perkins, State Geologist of Vermont. Perhaps the kindest thing that can be said for Perkins's work (1904, 1905, 1906) is that it introduced photographs of the Brandon fruits and seeds into the scientific literature and thereby brought renewed attention to an important fossil locality. From the botanical viewpoint, the venture was virtually valueless. Almost every minor variation in size, shape, and preservation was named as a "new species," and descriptions embodied little more than a statement regarding the dimensions and outline of each specimen. Hardly any new suggestions were made regarding the modern affinities of the fossils; instead, most of the "species" were placed in poorly defined form-genera. The largest nyssoid fruits were designated as *Glossocarpellites*, and others were classified as *Monocarpellites*, *Bicarpellites*, or *Tricarpellites*, depending upon the apparent number of carpels. As a result of this procedure, fruits that might very well have been borne on the same plant were assigned to different form-genera. Following Lesquereux, Perkins designated some of the smaller Brandon fruits as *Nyssa* — indeed, he listed 19 "species" of *Nyssa* — but we have found only a part of these to be nyssoid during our investigation.

For our own studies, we have had available a larger collection of specimens than Perkins possessed. Moreover, most of our material is better preserved than Perkins's material, for it has not been allowed to dry since its removal from the lignite. Whole fruits were collected by breaking chunks of lignite in the hands and keeping them moist until their transferral to the laboratory, where they were soaked for a few days in hydrofluoric acid or brushed vigorously to remove adhering quartz particles. (Physical and chemical characteristics of the lignite were discussed by Barghoorn and Spackman, 1950.) After prolonged washing in running water to remove the acid, the specimens were transferred to a solution of glycerine, ethanol, and water, in which they have been kept for several years.

We found it convenient to immerse individual specimens in a dish of water while examining them with the dissecting microscope. When dry specimens were desired for photographic or display purposes, we placed wet fruits under an inverted beaker and allowed them to dry out very gradually, for rapid desiccation produces cracks and other distortions. Internal structure was studied by means of microtome sections, some of the specimens being embedded in celloidin before cutting. The fossils were much softer and more easily sectioned than their modern counterparts.

In the systematic revision of the Brandon nyssas that follows, we have recognized four major morphological groups and have designated them as fossil species, making new nomenclatural combinations where necessary. In addition, we are assigning a new epithet to the Japanese fossil fruit previously called *Nyssa rugosa* by Miki (1956). We are very grateful to Professor Miki for sending specimens of this fossil and of other fossil nyssas from Japan so that we could compare them with our Brandon material.

Nomenclatural treatment of the Brandon fruits has been very much simplified by the location of the original specimens figured by Edward Hitchcock in 1853 and 1861 and by C. H. Hitchcock in 1862. This material was formerly housed in the American Museum of Natural History (see Perkins, 1904, p. 171) and was transferred to the U. S. National Museum in 1955. Through the cooperation of Drs. S. Mamay and J. A. Wolfe of the U. S. Geological Survey the specimens were examined several times during our investigation and some of them were photographed for inclusion in this paper. The fossils are carefully labelled with the numbers of the figures in Hitchcock's 1861 publication, and a comparison of the more distinctive specimens with Hitchcock's illustrations shows that they are indeed the figured fruits.

TAXONOMIC TREATMENT

1. *Nyssa brandoniana* (Lesq.) Eyde & Barghoorn, comb. nov.

FIGS. 1, 6, 7.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. 15: 97. fig. 1. 1853, Geol. Vt. 1: 229. figs. 111–116. 1861.

Carpolithes brandoniana Lesquereux, Am. Jour. Sci. II. 32: 356. 1861, in Hitchcock, Geol. Vt. 2: 713. 1861; Knowlton, Bull. Torrey Club 29: 640. pl. 25, figs. 1, 2, 11, 12. 1902; Perkins, Rep. Vt. State Geol. 4: 175. pl. 75, figs. 10, 11, 20. 1904.

Carpolithes elongatus Perkins, Rep. Vt. State Geol. 4: 176. pl. 75, figs. 1–3. 1904.

Carpolithes emarginatus Perkins, *ibid.* 177. pl. 75, fig. 4.

Carpolithes grandis Perkins, *ibid.* 178.

Carpolithes Hitchcockii Perkins, *ibid.* 179. pl. 75, fig. 19.

Carpolithes mucronatus Perkins, *ibid.* 179. pl. 75, figs. 15, 17.

Carpolithes obtusus Perkins, *ibid.* 177. pl. 75, figs. 5–8, 14.

Carpolithes ovatus Perkins, *ibid.* 178. pl. 75, fig. 9.

Carpolithes parvus Perkins, *ibid.* 179.

Carpolithes simplex Perkins, *ibid.* 178. pl. 75, fig. 12.

- Carpolithes solidus* Perkins, *ibid.* 179. *pl.* 75, *fig.* 18.
Carpolithes vermontanus Perkins, *ibid.* 179. *pl.* 75, *fig.* 13.
Glossocarpellites elongatus Perkins, Bull. Geol. Soc. Am. 16: 511. *pl.* 87, *fig.* 17. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 17. 1906.
Glossocarpellites obtusus Perkins, Bull. Geol. Soc. Am. 16: 511. *pl.* 87, *fig.* 16. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 16. 1906.
Glossocarpellites parvus Perkins, Bull. Geol. Soc. Am. 16: 510. *pl.* 86, *fig.* 15. 1905, Rep. Vt. State Geol. 5: 207. *pl.* 52, *fig.* 15. 1906.
Glossocarpellites grandis Perkins, Rep. Vt. State Geol. 5: 206. *pl.* 54, *figs.* 1-3. 1906.

Description.—Endocarps 25-45 mm. long, 18-30 mm. broad; rounded, elliptical, or obovate in outline; compressed in dorso-ventral direction. Unilocular, with conspicuous outline of germination valve usually extending slightly more than half the length of endocarp; valve narrower at base, wider above, tapering to acuminate apex. Surface of endocarp relatively smooth (sometimes warty in places) with occasional bits of leathery skin adhering to best-preserved specimens. Prominent mid-dorsal ridge present on upper half of valve, pits on both sides of dorsal ridge and at center of valve base indicating points where minor vascular strands passed from dorsal carpillary bundle into endocarp wall. Several longitudinal grooves at base of stone indicate former position of major peripheral bundles, and six or more pairs of grooves arching from sides of stone to placental region on flattened ventral surface indicate former position of ovular supply. Endocarp wall thinnest (about 2 mm.) near apex, thickest (more than 4 mm.) near base, composed of thick-walled fibers, as in modern *Nyssa*.

Material.—There are about 50 fruits and numerous fragments in the Paleobotanical Collections of the Botanical Museum, Harvard University (No. 56599). Most of these specimens have been kept in preservative, and some of them show remarkable retention of external details. Rapid drying evidently causes gaping of the valve and longitudinal splitting of the endocarp wall at the base of the dehiscence line, for such distortions are frequently encountered in material collected by earlier workers. Specimens figured by Hitchcock (1861) as figs. 111-117 and named *Carpolithes brandoniana* by Lesquereux are in the U. S. National Museum; all of these fruits are of the same kind except the one corresponding to fig. 117, which is a *Nyssa fissilis*. The specimens for Hitchcock's figs. 111-113 bear U. S. N. M. nos. 42066-42068. We have chosen U. S. N. M. 42067 as the lectotype.

Affinities.—The relatively smooth surface, the conspicuous valve margins, and the vascular pattern of *Nyssa brandoniana* are duplicated so closely in fruits of modern *N. javanica* that a close alliance of the two cannot be doubted. The fossils are much larger, to be sure, but the occurrence of the unusually large-fruited form "*N. megacarpa*" (the status of this plant is discussed by Eyde, 1963) proves that modern *Nyssa* has

not completely lost the genetic capacity for producing endocarps of exceptional size. The fossil differs from its modern counterpart in the possession of more massive ventral valve margins and in the greater number of placental strands visible on the ventral surface. Furthermore, marks of minor branches of the dorsal bundle are not commonly noticeable on the valve of *N. javanica* fruits. It is interesting that members of this alliance had already become unilocular in the early Tertiary; most other nyssas at that time produced fruits in which two or more locules were common.

The Miocene Latah formation has yielded an impression of a large fruit resembling modern *Nyssa javanica* in observable surficial features. A germination valve is not discernible with certainty, but the shape of the fruit, undulations of the relatively smooth surface, and imprints of transverse fibers are very suggestive of *N. javanica*. The specimen, U. S. N. M. 37012, was collected in Spokane, Washington, and figured and described by Knowlton (1926) as *Carpites magnifica*; Berry (1929) renamed it *Nyssa magnifica*. If this is indeed a *Nyssa* fruit, it is the closest fossil ally of *N. brandoniana*.

The fossil fruits *Palaeonyssa multilocularis* (Reid & Chandler, 1933; Chandler, 1961), and *P. spatulata* (Scott, 1954), from Eocene deposits of England and Oregon, respectively, share an important feature with *Nyssa brandoniana* and *N. javanica*, i.e., relative smoothness of the external surface. Other *Nyssa* fruits, fossil or modern, bear prominent ridges and grooves that have developed in association with vascular bundles supplying superior parts of the flower. In *N. brandoniana* marks of these peripheral bundles may be found on the basal part of the fruit, but at higher levels any sculpturing is associated with carpillary vasculature only. The "broad gently rounded ribs" mentioned by Reid and Chandler in their description of *P. multilocularis* (1933, p. 432) occur only opposite the septa and are associated with ventral carpellaries, rather than peripheral bundles; Scott's specimens were described as "at most slightly ridged." A possible phylogenetic relationship between *Palaeonyssa*, *N. brandoniana*, and *N. javanica* will be discussed along with the affinities of *N. fissilis*.

2. *Nyssa fissilis* (Lesq.) Eyde & Barghoorn, comb. nov.

FIGS. 2, 12–14, 23–25.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. 15: 98. figs. 2, 3, 6, 12. 1853,
Geol. Vt. 1: 229. figs. 117–128. 1861.

Carpolithes fissilis Lesquereux, Am. Jour. Sci. II. 32: 356. 1861, in Hitchcock,
Geol. Vt. 2: 713. 1861.

Carpolithes Grayana Lesquereux, Am. Jour. Sci. II. 32: 356. 1861, in Hitchcock,
Geol. Vt. 2: 714. 1861.

Carpolithes irregularis Lesquereux, Am. Jour. Sci. II. 32: 356. 1861, in Hitchcock,
Geol. Vt. 2: 714. 1861.

Fagus Hitchcockii Lesquereux, Am. Jour. Sci. II. 32: 357. 1861; in Hitchcock,
Geol. Vt. 2: 714. 1861.

Tricarpellites fissilis Knowlton, Bull. Torrey Club 29: 641. pl. 25, figs. 7, 8.
1902; Perkins, Rep. Vt. State Geol. 4: 188. pl. 77, figs. 61–64. 1904, Bull.
Geol. Soc. Am. 16: 512. pl. 87, fig. 19. 1905.

- Aristolochites apicalis* Perkins, Rep. Vt. State Geol. 4: 203. *pl.* 80, *fig.* 144. 1904.
- Bicarpellites Grayana* Perkins, *ibid.* 190. *pl.* 78, *fig.* 69.
- Bicarpellites Knowltonii* Perkins, Rep. Vt. State Geol. 4: 191. *pl.* 78, *figs.* 71, 72. 1904, Bull. Geol. Soc. Am. 16: 510. *pl.* 86, *fig.* 14. 1905, Rep. Vt. State Geol. 5: *pl.* 52, *fig.* 13. 1906.
- Bicarpellites obesus* Perkins, Rep. Vt. State Geol. 4: 191. *pl.* 78, *fig.* 75. 1904.
- Bicarpellites rotundus* Perkins, *ibid.* 191. *pl.* 78, *fig.* 76.
- Bicarpellites rugosus* Perkins, *ibid.* 191. *pl.* 78, *fig.* 70.
- Bicarpellites vermontanus* Perkins, *ibid.* 192. *pl.* 78, *figs.* 88, 89.
- Hicoria biacuminata* Perkins, *ibid.* 193. *pl.* 78, *figs.* 77, 81, Bull. Geol. Soc. Am. 16: 512. *pl.* 87, *fig.* 22. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 22. 1906.
- Hicoroides angulata* Perkins, *ibid.* 4: 183. *pl.* 76, *figs.* 28, 32, 33. 1904, Bull. Geol. Soc. Am. 16: 513. *pl.* 87, *fig.* 27. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 27. 1906.
- Hicoroides ellipsoidea* Perkins, Rep. Vt. State Geol. 4: 184. *pl.* 76, *fig.* 41. 1904, Bull. Geol. Soc. Am. 16: 513. *pl.* 87, *fig.* 26. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 26. 1906.
- Hicoroides globulus* Perkins, *ibid.* 4: 184. *pl.* 76, *figs.* 42, 43. 1904.
- Hicoroides parva* Perkins, *ibid.* 184. *pl.* 81, *fig.* 172.
- Hicoroides triangularis* Perkins, *ibid.* 183. *pl.* 76, *fig.* 40.
- Juglans brandonianus* Perkins, *ibid.* 182. *pl.* 76, *fig.* 36, Bull. Geol. Soc. Am. 16: 511. *pl.* 87, *fig.* 21. 1905, Rep. Vt. State Geol. 5: *pl.* 53. *fig.* 21. 1906.
- Monocarpellites elegans* Perkins, Rep. Vt. State Geol. 4: 181. *pl.* 76, *figs.* 25, 30. 1904.
- Monocarpellites gibbosus* Perkins, *ibid.* 181. *pl.* 76, *fig.* 26, Bull. Geol. Soc. Am. 16: 512. *pl.* 87, *fig.* 18. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 18. 1906.
- Monocarpellites Hitchcockii* Perkins, *ibid.* 4: 182. *pl.* 76, *fig.* 29. 1904.
- Monocarpellites irregularis* Perkins, *ibid.* 181. *pl.* 76, *fig.* 27.
- Monocarpellites medius* Perkins, *ibid.* 182. *pl.* 76, *fig.* 34.
- Monocarpellites orbicularis* Perkins, *ibid.* 181. *pl.* 76, *fig.* 24.
- Monocarpellites ovalis* Perkins, *ibid.* 182. *pl.* 76, *fig.* 35.
- Monocarpellites pyramidalis* Perkins, *ibid.* 180. *pl.* 76, *fig.* 22.
- Monocarpellites sulcatus* Perkins, *ibid.* 180. *pl.* 76, *fig.* 23, Bull. Geol. Soc. Am. 16: 512. *pl.* 87, *fig.* 20. 1905, Rep. Vt. State Geol. 5: *pl.* 53, *fig.* 20. 1906.
- Monocarpellites vermontanus* Perkins, *ibid.* 4: 182. *pl.* 76, *fig.* 35. 1904.
- Monocarpellites Whitfieldii* Perkins, *ibid.* 180. *pl.* 76, *fig.* 21.
- Tricarpellites acuminatus* Perkins, *ibid.* 190. *pl.* 78, *fig.* 83.
- Tricarpellites amygdaloideus* Perkins, *ibid.* 188. *pl.* 77, *fig.* 58.
- Tricarpellites angularis* Perkins, *ibid.* 187. *pl.* 77, *fig.* 57.
- Tricarpellites carinatus* Perkins, *ibid.* 186. *pl.* 77, *fig.* 47.
- Tricarpellites castanoides* Perkins, *ibid.* 187. *pl.* 77, *fig.* 54.
- Tricarpellites contractus* Perkins, *ibid.* 189. *pl.* 77, *fig.* 67.
- Tricarpellites Dalei* Perkins, *ibid.* 186. *pl.* 77, *fig.* 48.
- Tricarpellites elongatus* Perkins, *ibid.* 186. *pl.* 77, *fig.* 45.
- Tricarpellites fagooides* Perkins, *ibid.* 188. *pl.* 77, *fig.* 59.
- Tricarpellites hemiovalis* Perkins, *ibid.* 190. *pl.* 81, *fig.* 171.
- Tricarpellites inequalis* Perkins, *ibid.* 186. *pl.* 77, *fig.* 44.
- Tricarpellites lignitus* Perkins, *ibid.* 186. *pl.* 77, *fig.* 46.
- Tricarpellites major* Perkins, *ibid.* 189. *pl.* 77, *fig.* 66.
- Tricarpellites obesus* Perkins, *ibid.* 188. *pl.* 77, *fig.* 60.

- Tricarpellites ovalis* Perkins, *ibid.* 187. *pl.* 77, *fig.* 53.
Tricarpellites Pringlei Perkins, *ibid.* 189. *pl.* 77, *fig.* 68.
Tricarpellites rostratus Perkins, *ibid.* 187. *pl.* 77, *fig.* 52.
Tricarpellites rugosus Perkins, *ibid.* 187. *pl.* 77, *fig.* 55.
Tricarpellites Seelyi Perkins, *ibid.* 189. *pl.* 77, *fig.* 65.
Bicarpellites abbreviatus Perkins, *ibid.* 5: 209. *pl.* 56, *fig.* 1. 1906.
Bicarpellites attenuatus Perkins, *ibid.* 210. *pl.* 54, *fig.* 9.
Bicarpellites bicarinatus Perkins, *ibid.* 210. *pl.* 54, *fig.* 10.
Bicarpellites brevis Perkins, *ibid.* 213. *pl.* 55, *fig.* 13.
Bicarpellites carinatus Perkins, *ibid.* 210. *pl.* 54, *fig.* 11.
Bicarpellites crassus Perkins, *ibid.* 211. *pl.* 55, *figs.* 2, 3.
Bicarpellites crateriformis Perkins, *ibid.* 211. *pl.* 55, *fig.* 1.
Bicarpellites inequalis Perkins, *ibid.* 211. *pl.* 55, *fig.* 4.
Bicarpellites lanceolatus Perkins, *ibid.* 211. *pl.* 55, *fig.* 5.
Bicarpellites latus Perkins, *ibid.* 212. *pl.* 55, *figs.* 6, 7.
Bicarpellites major Perkins, *ibid.* 212. *pl.* 55, *figs.* 8, 11, 12.
Bicarpellites medioides Perkins, *ibid.* 212. *pl.* 55, *figs.* 9, 10.
Bicarpellites ovatus Perkins, *ibid.* 213. *pl.* 55, *fig.* 14.
Bicarpellites papillosus Perkins, *ibid.* 213. *pl.* 55, *fig.* 15.
Bicarpellites parvus Perkins, *ibid.* 214. *pl.* 55, *fig.* 16.
Bicarpellites quadrangulatus Perkins, *ibid.* 214. *pl.* 56, *fig.* 2.
Bicarpellites quadratus Perkins, *ibid.* 214. *pl.* 56, *fig.* 3.
Bicarpellites solidus Perkins, *ibid.* 215. *pl.* 56, *fig.* 4.
Bicarpellites sulcatus Perkins, *ibid.* 215. *pl.* 56, *figs.* 5, 6.
Hicoroides levis Perkins, *ibid.* 217. *pl.* 56, *fig.* 15.
Monocarpellites amygdaloides Perkins, *ibid.* 208. *pl.* 54, *fig.* 4.
Monocarpellites multicostatus Perkins, *ibid.* 208. *pl.* 54, *figs.* 5–7.
Monocarpellites pruniformis Perkins, *ibid.* 208. *pl.* 54, *fig.* 8.
Tricarpellites alatus Perkins, *ibid.* 216. *pl.* 56, *figs.* 11, 12.
Tricarpellites brandonianus Perkins, *ibid.* 217. *pl.* 56, *figs.* 13, 14.
Tricarpellites curtus Perkins, *ibid.* 216. *pl.* 56, *figs.* 7, 8.
Tricarpellites triangularis Perkins, *ibid.* 216. *pl.* 56, *figs.* 9, 10.

Description.—Endocarps 17–44 mm. long, 13–28 mm. broad, 5–15 mm. thick across inflated base; rounded, elliptical, ovate, or obovate in outline; flattened, elliptical, concavo-convex, or triangular in cross section; bearing a short apical mucro when well-preserved. Mostly bilocular, occasionally trilocular, perhaps also unilocular; triangular germination valves usually occupying somewhat less than half the length of endocarp. Surface divided into 10–15 prominent longitudinal ridges (sometimes obscured by compression or abrasion) and intervening grooves, with remnants of heavy vascular strands visible in places along crests of ridges. Fibrous endocarp wall up to 5 mm. thick.

Material.—There are about 750 fruits of this species among the Paleobotanical Collections of the Botanical Museum, Harvard University (*No. 56600*), exhibiting a very wide range of variability in size and shape. The dimensions given above include the largest and smallest specimens obtained from the lignite.

In addition, we have found two specimens of *Nyssa fissilis* (*No. 56601*)

among fruits taken from the silt that overlies the lignite (see Barghoorn & Spackman, 1950, for a description of this deposit). One of these silt fruits (FIGS. 23, 24) is the smallest *N. fissilis* we have seen, measuring 13 mm. in length and 9 mm. in breadth. The other (FIG. 25) has a very narrow outline — measuring 21 mm. in length and 7.5 mm. in diameter — and unusually sharp ridges. The silt specimens are of special interest, for they illustrate the differences in form that can be brought about by differences in compressional conditions. Apparently the fruit called *Aristolochites apicalis* by Perkins (1904, fig. 144) is also a *Nyssa fissilis* from the Brandon silt. We have found the figured fossil, bearing Perkins's label, among material sent to us by the Vermont State Museum, and it is similar to our smaller silt specimen.

We have chosen *U. S. N. M. 42071*, the specimen shown as fig. 118 in Hitchcock's 1861 report, as the lectotype for this species.

Affinities. — The most distinctive feature of the fruit of *Nyssa fissilis* is the position of its peripheral vascular bundles on the crests of the ridges. Since compression and abrasion frequently obscure this feature, it is fortunate that we were able to examine such a large collection of specimens. Apparently Perkins had observed the marks of the peripheral strands when, in a rare moment of descriptive zeal, he mentioned "rows of papillae" along the ridges of his "*Bicarpellites papillosus*" (1906, p. 213). Since the only modern *Nyssa* fruit in which ridges and bundles are similarly associated is that of *N. aquatica*, it is not unreasonable to infer an affinity between *N. aquatica* and *N. fissilis*.

One finds in *Nyssa fissilis* just those differences that might reasonably be expected if this fossil really is ancestrally related to the unilocular fruit of *N. aquatica*: both locules and peripheral bundles are more plentiful. (It follows that the appendages supplied by peripheral bundles were also more numerous in the flower from which the *N. fissilis* fruit developed than in the modern counterparts.) We are not sure whether any of the fossils are unilocular. Many of them appear to be unilocular when cut in half (hence Perkins's designation *Monocarpellites*), but whenever we have examined microtome sections of such specimens, we have found a tightly closed abortive locule in addition to a fertile one. The *N. fissilis* population was evidently one in which the ovary was undergoing reduction from a trilocular to a bilocular condition: distinctly three-sided fruits are common, but many of these completely lack a third locule.

Past attempts by various authors to compare fossil *Nyssa* fruits with fruits of *N. aquatica* have had no morphological basis. Impressions and coalified fruits combined under the name *N. hesperia* (Chaney & Axelrod, 1959) have been examined during our investigation; and we find that they bear broad rounded ridges with vascular bundles in intervening grooves, as in the modern *N. sylvatica* complex. These features are very well preserved in specimens collected from the Latah formation (*U. S. N. M. 38653, 38654*, and some specimens without numbers) and in material from the Mascall and Weaverville floras that was sent to us for inspection through

the courtesy of Dr. Wayne L. Fry of the University of California Museum of Paleontology (*U. C. M. P.* 1071, 3231, & 1275). A fruit from the Citronelle formation in southern Alabama was designated as *N. aquaticaformis* by Berry (1916b, pp. 203, 204; Pl. 47, fig. 8) because of a supposed resemblance to *N. aquatica*. An inspection of Berry's figured specimen has shown, however, that the fruit is in all observable features — size, shape, and papery wings — identical with fruits of modern *N. ogeche*. Berry believed the fossil to be of Pliocene age, but geological opinion has more recently favored a Pleistocene age for the Citronelle formation (Fisk, 1945; Doering, 1958). Since "*N. aquaticaformis*" was collected within or almost within the western limits of the present *N. ogeche* range, the finding is of little importance.

On the other hand, a Miocene fruit found in the Zittau Valley of central Europe and compared by Czeczott and Skirgiello (in Czeczott, Zaléwska, & Skirgiello, 1959) with modern *Nyssa ogeche* looks much more like *N. aquatica*. The better of two specimens, which the Polish authors show in Pl. 7, fig. 20, of their work, bears three prominent ridges on the side of the fruit where the vague outline of a valve can be seen; these ridges occupy the same positions with respect to the valve as would the dorsal ridge and two flanking ridges of a modern *N. aquatica* stone. The Zittau Valley fossil is not well-preserved and the authors cautiously call it "?*Nyssa* sp.". If the suggested identification is correct, this fruit is probably an intermediate between *N. fissilis* and *N. aquatica*.

Many of the three-sided specimens of *Nyssa fissilis* resemble *Palaeonyssa* in size and shape, but the valves of the Brandon fossils are generally triangular in outline, while those of *Palaeonyssa* are oval. Moreover, *Palaeonyssa* fruits do not have 10–15 ridges such as one finds on the surface of *N. fissilis*. It seems unlikely that the relative smoothness of all known *Palaeonyssa* specimens is due to abrasion alone. We prefer to view the three- or four-locular *Palaeonyssa* as representing a primitive smooth-surfaced condition from which the ridged and furrowed *N. fissilis* fruit has evolved. This change could have come about through increasing fusion of peripheral bundles with carpellaries in the ancient flowers that produced these fruits, and a consequent greater influence of the peripherals on the development of the woody endocarp. Evidence for such change has been found in flowers of modern Nyssaceae.

In the first author's previous paper it was concluded that the modern species *Nyssa javanica* and *N. aquatica* are more closely related to each other than either one is to members of the *N. sylvatica* complex. This relationship between *N. javanica* and *N. aquatica* could be explained by assuming that *Palaeonyssa* is ancestral to both. In this view, *N. brandoniana* and *N. fissilis* would be regarded as intermediates in the divergence, *N. fissilis* representing a stage about halfway between *Palaeonyssa* and *N. aquatica* and *N. brandoniana* being much more like its modern counterpart, *N. javanica*. This view would require a more rapid reduction in the number of locules along the line that produced *N. javanica* and a slower

reduction in the number of locules along the line that produced *N. aquatica*, ultimately resulting in a unilocular ovary in each.

3. *Nyssa complanata* Lesquereux

Figs. 5, 15-19.

Unnamed fruit, E. Hitchcock, Am. Jour. Sci. II. 15: 100. figs. 13, 14. 1853, Geol. Vt. 1: 231. figs. 153, 154. 1861.

Nyssa complanata Lesquereux, Am. Jour. Sci. II. 32: 361. 1861, in Hitchcock, Geol. Vt. 2: 717. 1861; Perkins, Rep. Vt. State Geol. 4: 198. pl. 79, fig. 112. 1904, *ibid.* 5: 219. pl. 57, figs. 3, 5. 1906.

Nyssa microcarpa Lesquereux, Am. Jour. Sci. II. 32: 361. 1861, in Hitchcock, Geol. Vt. 2: 717. 1861; Perkins, Rep. Vt. State Geol. 4: 194. pl. 79, fig. 90. 1904.

Bicarpellites minimus Perkins, *ibid.* 192. pl. 78, fig. 79.

Nyssa curta Perkins, *ibid.* 199. pl. 79, fig. 111, *ibid.* 5: 219. pl. 57, figs. 4, 6. 1906; Berry, U. S. Geol. Surv. Prof. Paper 92: 125. pl. 19, fig. 10. 1930.

Lescuria attenuata Perkins, Rep. Vt. State Geol. 5: 220. pl. 57, figs. 7-10. 1906.

Description. — Endocarp 5.6-11.8 mm. long, 3.2-8.8 mm. broad; mostly ovate or elliptical in outline. Locules two to four, with triangular valves confined to upper half of endocarp. Surface bears 10-15 rounded longitudinal ridges with remains of vascular bundles in intervening grooves. Internal vascular pattern visible in cross sections, conforming to pattern in modern *Nyssa sylvatica* complex except for presence of additional strands in axis at base. Endocarp wall up to 800μ thick, composed of single inner layer of longitudinal fibers surrounded by narrow zone of circumlocular fibers and outer region where aggregates of fibers run in many directions.

Material. — More than 250 specimens of *Nyssa complanata* in the Paleobotanical Collections of the Botanical Museum, Harvard University (No. 56602) were inspected and measured in the course of our work, many of which were extremely fragile and, consequently, crumbled when handled. This fragility is partly due to evaporation of the preserving fluid on the museum shelf, followed by fungus attack, and partly due to the structure of the endocarp wall itself. Splitting of the dorsal wall along the mid-dorsal groove is quite common, and transverse sections show that in most specimens the septa are ruptured. The deformation that accompanies septal collapse frequently makes it impossible to ascertain by external examination the number of locules in a fruit. There are flattened fruits in our collection that appear beyond doubt to be unilocular, but whenever we have sectioned one of these, we have found a second or even a third locule. A few specimens have a five-faced appearance, but sectioning has shown this condition to be a compressional distortion of a four-celled fruit. As a matter of curiosity, however, we have separated our collection on the basis of external appearance and found 118 (46 per cent) "trilocular," and 101 (39 per cent) "bilocular," and 39 (15 per cent) "four-locular."

The holotype for *Nyssa complanata* (U. S. N. M. 42074) is the fruit shown as fig. 153 in Hitchcock's 1861 work. Our FIG. 5 is a photograph of

this specimen and another to which Lesquereux assigned the name "*N. microcarpa*" (*U. S. N. M.* 42073).

Affinities. — The nearest living equivalents of *Nyssa complanata* are members of the modern *N. sylvatica* complex. The fossils differ from their modern counterparts in those respects which might be anticipated in an ancestral member of this alliance: they are multilocular and have more numerous peripheral vascular bundles. The internal vascular supply appears as dark spots in thick sections taken from the better specimens, with the same pattern as that found in the modern fruits except for the occurrence of a few extra strands in some of the fossils. These strands run longitudinally in the basal part of the axis along which the septa are united, and they diminish and disappear after a short distance. They can best be interpreted as remnants of a receptacle tip extending slightly beyond the bases of the carpels. We have not found similar strands in modern nyssas. Another interesting feature of the fossils is the lobed appearance of sections taken from the basal part of some of the three- or four-locular fruits (FIG. 18). In such sections the carpels seem to retain their distinctness more than in sections taken at higher levels in the fruit. Histologically, the fossils are somewhat more comparable to bilocular fruits of *N. sinensis* than to fruits of *N. sylvatica*, for the thick ventral wall of unilocular *N. sylvatica* has no exact counterpart among the fossils. Except for the greater breadth of some compressed specimens, the size of the fossils falls within the range of variation found in the modern *N. sylvatica* complex.

Fossils morphologically similar to *Nyssa complanata* have been collected in many countries of the northern hemisphere from horizons that range from lower Eocene to upper Pliocene in age. The small lignitized *Nyssa* stone from the Eocene Wilcox flora that Berry (1930) assigned to Perkins's *N. curta* is indistinguishable from the smaller Brandon specimens; therefore, we have transferred it to *N. complanata*. The name *N. wilcoxiana* Berry (1916a, 1930, 1941) has been applied to a number of other Eocene fossils from the southeastern United States, some of which, though poorly preserved, resemble *N. complanata* in gross features. Two impressions figured by Berry (1930, Pl. 19, figs. 7 & 8) and entered in the collections of the National Museum as *U. S. N. M.* 39920 are possibly related to the Brandon species; however, there is insufficient retention of detail in these specimens even for certain identification as *Nyssa*. A more convincing impression (*U. S. N. M.* 36361), collected at "Station 20, Wilcox group" and identified by Berry as *N. wilcoxiana*, measures 13 mm. in length, 8 mm. in breadth, and shows the outline of a germination valve and a ribbed surface; it is likely that an impression of *N. complanata* would be very similar in appearance. The fossil fruits collected in the western United States and known as *N. hesperia* (previously discussed in this article) and *N. californica* MacGinitie (1941) are very much like *N. complanata* except for their somewhat greater size. The specimens of *N. hesperia* that we have inspected range from 10–18 mm. in length.

Fossil *Nyssa* fruits have been found in a great many localities on the European continent (TABLE I), particularly in brown coal deposits. With the exception of the rare form from the Zittau Valley that we have discussed under the affinities of *N. fissilis*, all of these fossils are allied to the modern *N. sylvatica* complex. In the older literature a variety of names were assigned to these remains, but Kirchheimer, who has been the principal investigator of European Tertiary fruits and seeds, was unable to find specific distinctions; therefore he combined all of these fossils into one fossil species, *N. disseminata* (Kirchheimer, 1938). In recent years, the name *N. disseminata* (Ludwig) Kirchheimer has been applied to almost all fossil *Nyssa* fruits found in continental Europe. The name has also been applied to all similar remains found in Asiatic U. S. S. R. (TABLE I), except for a recent finding from Oligocene deposits along the Tavda River, which Dorofeyev (1961) has designated as *N. macrocarpa*. Unfortunately, Dorofeyev's announcement of this finding includes only the new name and some illustrations (Pl. I, figs. 29-32) without an accompanying description of size and distinguishing features. It is not clear from the figures how the Tavda River fossil is to be separated from *N. disseminata*. Even if the proposed new species does differ in some important respect, it will have no status under the rules of nomenclature until some sort of description has been published.

Kirchheimer, in 1938 and again in 1957 (pp. 572, 573), has discussed variation in *Nyssa disseminata*. Fossils from the Oligocene and Miocene are usually larger (up to 22 mm. long) than Pliocene specimens (as little as 5 mm. in length). Furthermore, only the unilocular condition has been reported for Pliocene fruits, whereas a minority of the older fruits are bilocular and occasionally trilocular. *Nyssa* fruits with four locules have not yet been noted among the continental European collections. Thus, the *N. complanata* population differs from *N. disseminata* by virtue of its greater average number of locules. There are also differences in average size between early Tertiary specimens of *N. disseminata* and the Brandon population. In other respects, however, the two are quite similar and isolated fruits of *N. complanata* would surely be called *N. disseminata* if they had been collected in a European brown coal.

British authors have preferred to maintain separate names for fossil fruits of the *Nyssa sylvatica* alliance rather than to unite them with the brown coal species. E. M. Reid (1927) described as *N. oviformis* two silicified fruits collected from a presumably Eocene locality in Brittany. The excellently preserved specimen shown in Pl. I, fig. 4, of Mrs. Reid's paper bears a marked resemblance in thickness and outline to a large bilocular stone of modern *N. sinensis*. There are apparently no notable differences between these French fossils and the London Clay fruits described as *Protonyssa bilocularis* by Reid and Chandler in 1933 (changed to *Nyssa bilocularis* by Chandler, 1961). Miss Chandler (1957) used the name *N. boveyana* for lignitized endocarps found in the Oligocene Bovey Tracey lignite, material that is similar in size and general features to modern *N. sylvatica* and to *N. disseminata*. The small pyritized fruit

described by Miss Chandler as *N. cooperi* in her recent revision of the London Clay flora (1961) seems also to belong with this alliance, since its major vascular bundles, wherever visible, are seen to lie in longitudinal grooves. This fossil bears an interesting resemblance to *N. complanata* in size (9.5 mm. long and 6.25 mm. broad) and in the possession of three locules. Unfortunately, only one specimen of *N. cooperi* is presently known.

Pliocene fruits allied with the *Nyssa sylvatica* complex collected at a number of localities in Japan were thoroughly reviewed by Miki (1956). These fruits are so similar to *N. sylvatica* that Miki has used that name in describing them. It is peculiar that all of these fossils are unilocular, since the modern *Nyssa* population geographically closest is the frequently bilocular *N. sinensis* of China.

In view of the general similarity of all of the fossils discussed in this section and their dissimilarity to those discussed in preceding sections, it seems we are dealing here with a natural group — an evolutionary alliance established in the early Tertiary (*Nyssa cooperi*, *N. complanata*) from which the closely related modern species (*N. sinensis*, *N. sylvatica*, and *N. biflora*) have evolved. It can hardly be expected that all members of this alliance would fall into a direct line of descent. Indeed, there must have been numerous instances of divergence, speciation, and extinction during the course of the Tertiary, and a part of the variation in size and minor features found in the fossil record of this group may be attributed to such events. Considering the variation encountered in fruits collected from modern members of the alliance, however, it is unlikely that we can detect any evolutionary changes save the broader ones such as reduction in number of locules.

The newly described *Nyssoidaea eocenica* (Chandler, 1962), found in middle Eocene strata of southern England, may possibly be related to this same general alliance, since it has a similar arrangement of ridges and vascular bundles and bears a superficial resemblance to members of the modern *Nyssa sylvatica* complex. However, *Nyssoidaea eocenica* is characterized by a short germination valve and by an internal dorsal ridge on the endocarp wall, a feature unknown in *Nyssa* species.

4. *Nyssa lescurii* (C. H. Hitchcock) Perkins FIGS. 3, 4, 8, 27, 28.

Carpolithes Lescurii C. H. Hitchcock, Proc. Portland Soc. Nat. Hist. 1: 95. pl. 1, fig. 5. 1862.

Nyssa ascoidea Perkins, Rep. Vt. State Geol. 4: 196. pl. 79, fig. 96. 1904.

Nyssa Clarkii Perkins, *ibid.* 199. pl. 81, fig. 167.

Nyssa crassicostata Perkins, *ibid.* 196. pl. 79, fig. 97, Bull. Geol. Soc. Am. 16: 509. pl. 86, fig. 11. 1905, Rep. Vt. State Geol. 5: pl. 52, fig. 11. 1906.

Nyssa elongata Perkins, Rep. Vt. State Geol. 4: 197. pl. 79, fig. 102. 1904.

Nyssa equicostata Perkins, *ibid.* 198. pl. 79, fig. 110.

Nyssa excavata Perkins, *ibid.* 199. pl. 81, fig. 166.

Nyssa Jonesii Perkins, *ibid.* 197. pl. 79, fig. 101, Bull. Geol. Soc. Am. 16: 509. pl. 86, fig. 8. 1905.

- Nyssa lescurii* Perkins, Rep. Vt. State Geol. 4: 197. *pl.* 79, *fig.* 100. 1904, Bull. Geol. Soc. Am. 16: 509. *pl.* 86, *fig.* 9. 1905, Rep. Vt. State Geol. 5: 218. *pl.* 52, *fig.* 9; *pl.* 57, *fig.* 2. 1906.
Nyssa multicostata Perkins, *ibid.* 4: 197. *pl.* 79, *fig.* 103. 1904.
Nyssa ovata Perkins, *ibid.* 196. *pl.* 79, *fig.* 98.
Nyssa acuticostata Perkins, *ibid.* 5: 218. *pl.* 56, *figs.* 16, 17. 1906.
Nyssa rugosa sensu Kräusel, Jahrb. Preuss. Geol. Landesanstalt 39: 387. 1918, in part, not Weber, Palaeontographica 2: 185. *pl.* 20, *fig.* 10. 1852.

Description. — Endocarp 13.5–24 mm. long, 7–13.5 mm. broad; elliptical or ovate in outline; often almost rounded in cross section. Short conical projection at apex is encircled by irregular line of detachment of perianth lobes. Unilocular or bilocular (both conditions common); germination valves confined to apical half, not usually visible externally. Surface divided into 10–15 (occasionally more) mostly rounded ribs with vascular strands traversing intervening grooves. Transverse fibrous elements composing outer part of endocarp wall visible on surface of broadest ribs. Endocarp wall up to 3 mm. thick (often thickest along dorsal midline of valve); fibrous internal tissues greatly compressed. Only the thick outer cell walls of the outermost integumentary cell layer remain in the tightly shut locules.

Material. — The Paleobotanical Collections of the Botanical Museum, Harvard University, contain almost 50 specimens (all catalogued as No. 56603), many of them broken. Fruits of this kind have been collected only from the Brandon silt; i.e., they have not been found in the lignite body itself. Conversely, other fossil species of *Nyssa* have not been encountered in the silt, except for the two examples of *N. fissilis* mentioned earlier. This is a rather peculiar circumstance, since deposition of the Brandon silt is believed to have followed deposition of the lignite without any great intervening lapse of time (Traverse, 1955, p. 34).

It is evident that these fruits have been compressed in a different manner from the nyssas found in the lignite. Most specimens are flattened little or not at all, and there is no concavity of the dorsal region to mark the position of the germination valve. The fibrous tissue has a very dense appearance in cross section, all or most of the lumina in the elements having been obliterated.

Apparently there were no fruits of this kind among Edward Hitchcock's original collections. The first description is that of C. H. Hitchcock (1862), who was geologist for the state of Maine. The holotype (U. S. N. M. 42072) is the specimen figured with this description; it is one of the largest examples of *Nyssa lescurii* that we have seen (FIG. 4).

Affinities. — These fossils have features in common with fossil and modern members of the *Nyssa sylvatica* alliance, a fact which led Kräusel (1918) to unite them with the nyssas of the German brown coal as a single fossil species. *Nyssa lescurii* is distinguishable from members of that alliance, however, by means of its thick endocarp wall, its conical apical

projection, and its greater size. Specimens of *N. complanata*, for instance, are not nearly so long nor so massive as those of *N. lescurii*, and it is impossible to confuse the two.

A further difference between *Nyssa lescurii* and *N. complanata* can be seen when cross sections are compared under the microscope. The locule in *N. complanata* is lined by a single layer of longitudinal fibers, surrounded by a zone of transverse fibers arranged circumferentially around the locule, but sections taken from *N. lescurii* show several layers of longitudinal fibers between the locule and the zone of circumlocular fibers. The latter arrangement seems to prevail in *N. fissilis* and *N. brandoniana* also; whereas the fruits of modern *Nyssa* species all seem to have a layer of longitudinal fibers that is only one cell thick at most places in the endocarp.

The apical region of these fruits is distinctive. Remains of the disk and of the rim along which calyx and corolla lobes were situated are not seen in other Brandon nyssas. The conical projection is suggestive of a similar structure to be found in flowers and fruits of *N. ogeche* and possibly indicates a relationship between *N. lescurii* and this modern species. The only other fossil *Nyssa* fruit that we have seen on which the vestige of a conical disk is present is *N. pachycarpa* Miki (1956), a thick-walled bilocular fruit from the Japanese Pliocene (FIG. 26). Specimens of *N. pachycarpa* tend to be more flattened than those of *N. lescurii*, but otherwise the two fossils are very much alike. The fruit shown in cross section as item N(a) of Miki's fig. 5 seems to be compressed in the same manner as the fossils from the Brandon silt, the thickness of the endocarp wall being exaggerated along the center of the valve. Item N(b) of this same figure shows a contrasting cross section from another fruit in which the valve is much thinner.

A number of fossils having points in common with *Nyssa lescurii* have been acquired from early Tertiary beds of the southern United States. Some of these have been reported in the literature as *N. wilcoxiana* Berry, a name that has been applied to an assortment of remains that differ considerably in their observable features. An impression (*U. S. N. M.* 39922) taken from the Eocene Holly Springs sand and figured by Berry in 1930 (Pl. 39, figs. 8, 9) resembles *N. lescurii* in size and shape, as also does a coalified fruit from the Claiborne flora of Smithville, Texas (mentioned by Berry in 1924, p. 89). The latter specimen is shown in our FIGS. 21 and 22. Another fossil with similar characteristics is the impression (*U. S. N. M.* 35979) from the Wilcox flora that Berry called *N. eolignitica* (1916a, Pl. 99, fig. 8). The Claiborne and Jackson floras include molds known as *N. texana* Berry that may appropriately be discussed here because of their resemblance in ellipsoidal shape and broad ribbing to *N. lescurii*. During our comparative review we have examined the material originally figured by Berry (1924, Pl. 22, fig. 5 & Pl. 39, fig. 3) and now in the National Museum as *U. S. N. M.* 38332 and 38387, and some additional collections, not previously reported, have been made available to us through the courtesy of Dr. Jack Wolfe of the U. S. Geological Survey. The latter material includes fruit molds from the vicinity of Columbus,

Kentucky, and from Trinity County and Karnes County in Texas; according to Dr. Wolfe, the strata from which these collections were made are of Oligocene age. All of the molds are very much alike except for slight variations in size: Berry's figured specimens are about 30 mm. long; those from Kentucky and Trinity County are 22–27 mm. long; and the better of two molds from Karnes County is 19 mm. long (FIG. 20). Identification as *Nyssa* is secure, because casts of the locules are nicely preserved in the Trinity County material, and the outline of the germination valve is occasionally quite clear (FIG. 10). The great abundance with which the molds occur in the sandstone matrix is impressive, especially at the Trinity County locality, where molds of mastixioid fruits as well as nyssoid fruits are present (FIG. 9). The molds are larger than the lignitized *N. lescurii* fruits, and there is no evidence of an apical projection or of a second locule. Moreover, the marks of the vascular bundles in the 12–15 longitudinal grooves are thicker in the molds — perhaps owing to the former presence of multiple strands in each groove — than they are in *N. lescurii*. Some of these differences could be due to differences in preservation, however. For instance, molds would not be expected to reveal the bilocular condition if a second locule were abortive and tightly shut by compression.

Although all of the fossils mentioned in this discussion might conveniently be combined into one morphological category on the basis of superficial similarities in size and general appearance, it is doubtful whether they constitute a natural group. Judging by the relationship between ridges and vascular bundles, each of these forms is more closely related to the *Nyssa sylvatica* alliance than to *Palaeonyssa*, *N. brandoniana*, *N. fissilis*, etc. It is probable, however, that none of these forms is as closely allied to *N. sylvatica* and its antecedents as are the forms discussed under the affinities of *N. complanata*. Possibly *N. lescurii* or one of the other fossils that we have discussed here is ancestrally related to the puzzling modern species *N. ogeche*; it is also possible that all of these forms belong to evolutionary lines that have terminated in extinction.

5. *Nyssa aspratilis* Eyde & Barghoorn, nom. nov.

FIG. 11.

Nyssa rugosa Miki, Jour. Inst. Polytech. Osaka Univ. D. 7: 287. *text-fig. 5, A–F; pl. 1, fig. D.* 1956, not Weber, Palaeontographica 2: 185. *pl. 20, fig. 10.* 1852.

Remarks. — The new name is applied to larger (20–24 mm. long) bilocular endocarps from the Japanese Pliocene that differ from *Nyssa pachycarpa* in the extreme rugosity of their surfaces. The name *Nyssa rugosa* cannot be used for these fruits, because this combination was validly published more than a century ago by Weber as a designation for certain fossils of the German brown coal (see Kirchheimer, 1938, for discussion and references). When we brought this point to the attention of Professor Miki during his visit to Harvard in 1959, he requested that we make the necessary nomenclatural change in our review.

The affinities of *Nyssa aspratilis* are difficult to ascertain, because the roughness of the surface obscures the marks of major vascular bundles. One specimen shows evidence of a median dorsal ridge (FIG. 11), indicating a relationship with *N. aquatica* and *N. javanica*. The ridge is not visible in other specimens that we have seen, however.

REJECTED AND DOUBTFUL FORMS

- Nyssa cylindrica* Perkins, Rep. Vt. State Geol. 4: 195. *pl. 79, fig. 91.* 1904.
Nyssa gracilis Berry, Jour. Geol. 17: 29. *fig. 10.* 1909.
Nyssa jacksoniana Berry, U. S. Geol. Surv. Prof. Paper 92: 192. *pl. 65, fig. 7.* 1924; Ball, Bull. Agr. Mechan. Coll. Tex. IV. 2: 168. *pl. 24, fig. 7.* 1931.
Nyssa laevigata Lesquereux, Am. Jour. Sci. II. 32: 361. 1861, in Hitchcock, Geol. Vt. 2: 717. 1861.
Nyssa lamellosa Perkins, Rep. Vt. State Geol. 4: 195. *pl. 79, figs. 93, 94.* 1904.
Nyssa solea Perkins, *ibid.* 194. *pl. 78, fig. 78.*

The fossils listed by Perkins as *Nyssa cylindrica*, *N. lamellosa*, *N. laevigata*, and *N. solea* have not been disposed of in the foregoing nomenclatural treatment. *Nyssa cylindrica* Perkins is a fragmentary specimen of doubtful affinity, and *N. laevigata* Lesquereux is apparently a fossil *Symplocos*. These names were applied to fossils figured by Hitchcock in 1861 (as figs. 155 and 156, respectively); the original specimens are in the National Museum. We have not seen the original fruits figured by Perkins as *N. solea* and *N. lamellosa*, but Perkins's photographs are matched by fruits in our own collections; hence we have been able to establish the identity of both. *Nyssa solea* may confidently be referred to *Symplocos*, a genus that is well represented at Brandon by pollen as well as fruit remains. Perkins compared *N. lamellosa*, a large fruit with very thick longitudinal wings, to modern *N. ogeche*, and Reid and Chandler accepted the supposed affinity of this fossil to *Nyssa* "without hesitation" (1933, p. 431). We had not investigated the internal structure at the time Professor Miki visited the Harvard laboratory and suggested a comparison with *Mellioidendron*, a styracaceous genus that is encountered in the Japanese lignites. Subsequently we prepared some microtome sections from one of two examples of *N. lamellosa* in our collection and found that the internal structure is very unlike that of *Nyssa*. A preliminary comparison with sections taken from a *Mellioidendron* fruit suggests that *N. lamellosa* is indeed a close relative of modern *Mellioidendron*.

In the course of our review, we have also examined two fossils from the southern United States that have been referred to *Nyssa* without adequate evidence. The Miocene impression from Virginia described and figured by Berry as *N. gracilis* is not at all convincing, and the same may be said for the single specimen of *N. jacksoniana* Berry that we were able to examine. The latter, bearing no. 1345, Collection of the A. & M. College of Texas, was kindly sent on loan by Dr. F. W. Gould of that institution; it is one of the fossils from the Fayette formation of Texas that Ball described as *N. jacksoniana* Berry. The eight to ten impressions seen on this specimen

bear ridges that are much finer and more numerous than those of a *Nyssa* stone, and there is no sign of a germination valve. We have not been able to locate the fossils originally figured as *N. jacksoniana* by Berry.

It is unfortunate that remains of fruits of *Camptotheca* or *Davidia* have not yet been correctly identified in the fossil record. The thick walled bi- or trilocular fruit called *Camptotheca crassa* by C. and E. M. Reid (1915, Pl. 14, figs. 1, 3, 4) is not at all like the thin-walled unilocular endocarp of modern *Camptotheca*. Moreover, the hard bony wings mentioned by the Reids in their description of the fossil can hardly be compared with the "wings" of *Camptotheca*, which are the dried outer fleshy tissues of the fruit wall. According to Kirchheimer (1957, p. 184), "*Camptotheca crassa*" is a fossil *Halesia*. Pliocene beds of Japan have yielded fruits designated as *Paleodavidia multipterium* (Miki, 1956), but Professor Miki has informed us in conversation that these remains were incorrectly identified and that they will subsequently be transferred to Styracaceae.

THE PLEISTOCENE RECORD

Pollen of Nyssaceae is not often reported from Pleistocene localities that are beyond the present distributional limits of the family. European palynologists have observed that deposits of Reuverian age (accepted as upper Pliocene by most palynologists) characteristically contain pollen of *Fagus*, *Nyssa*, *Sciadopitys*, *Liquidambar*, *Carya*, *Pterocarya*, and *Tsuga*, as well as pollen of the *Taxodium* type and the *Sequoia* type; of this list, only *Carya*, *Pterocarya*, and *Tsuga* continue into overlying beds of Teglian (lower Pleistocene) age (Rein, 1955; Florschütz, 1956; Zagwijn, 1960). Similar observations have been made in Japan, and strata of uncertain age are frequently classified on this basis, those containing pollen of *Nyssa*, Taxodiaceae, and *Liquidambar* being assigned to the Tertiary, and higher strata lacking these groups being assigned to the Pleistocene.

Notwithstanding, there are a few records of nyssaceous pollen in European deposits presumed to be Pleistocene. For instance, Szafer (1954), while investigating Pliocene and Pleistocene plant remains in southern Poland, found *Nyssa* pollen in horizon "Mizerna III," which he considers a part of the oldest interglacial interval. Nyssaceous pollen has also been recorded from interglacial strata of Italy (Paganelli, 1960) and of White Russia (Makhnach, 1957; Tsapenko & Makhnach, 1959, pp. 101, 118). The possibility of redeposition of Tertiary sediments is often acknowledged by workers who encounter a limited amount of typically Tertiary pollen in a Pleistocene horizon; on the other hand, it does not seem necessary to assume that *Nyssa* was completely exterminated in Europe during the first glaciation. The argument for the continuation of *Nyssa* in Europe — at least locally — during a part of the Pleistocene would be strengthened considerably by the discovery of fruit remains in sediments known to have been deposited after the first glaciation. As far as we are aware, however, the only findings of Pleistocene endocarps have been made in the southeastern United States (Berry, 1952), where *Nyssa* trees are plentiful today.

Although the fossil record does not yet reveal the pattern of Pleistocene extermination that resulted in the present disjunct distribution of the Nyssaceae, the evidence is abundant that the family was widely distributed on the northern continents from the beginning of the Tertiary until the advent of the Ice Age. To judge from the variety of forms found in the London Clay, in the Brandon deposits, and in the Japanese Pliocene beds, the number of well-marked species has commonly been as great or greater in past epochs than it is today. We may look forward to additional paleobotanical findings — hopefully in strata of Cretaceous age — that will extend our knowledge of this interesting family deeper into the past and increase our understanding of the relationships between the Nyssaceae and other groups of angiosperms.

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EXPLANATION OF PLATES

PLATE I

Figs. 1–5. Fossil *Nyssa* stones from Brandon. FIG. 1. *N. brandoniana*, specimens figured by Hitchcock in 1861; center specimen is holotype (U. S. N. M. 42067). FIG. 2. *N. fissilis* from type collection, mounted on card and bearing original label; holotype on left above (U. S. N. M. 42071). FIG. 3. *N. lescurii*, Brandon lignite, showing variation in size and shape. FIG. 4. *N. lescurii*, holotype (U. S. N. M. 42072). FIG. 5. *N. complanata* from Hitchcock's collection; holotype (U. S. N. M. 42074) on left; fruit on right is original "*N. microcarpa*" of Lesquereux. FIGS. 1–3, natural size; FIGS. 4 & 5, $\times 2$.

PLATE II

Figs. 6–12. FIGS. 6 & 7. *Nyssa brandoniana*, $\times 2.7$, Brandon lignite — note median ridge and marks of minor vascular strands on valves. FIG. 8. *N. lescurii*, $\times 5$, from Brandon, cut to show exaggerated thickness of endocarp wall at center of valve. FIG. 9. Molds of nyssoid and mastixioid endocarps in sandstone matrix, $\times \frac{1}{2}$; Oligocene, Trinity Co., Tex. FIG. 10. Smaller specimen, $\times 1$, same locality, showing locule cast of *Nyssa* fruit. FIG. 11. *N. aspratilis*, $\times 2.4$, from Japan — note rough surface and median dorsal ridge. FIG. 12. Apical view, $\times 2$, of three-sided *N. fissilis* (Brandon lignite), showing two open valves; third locule is often lacking in such stones.

PLATE III

FIG. 13. *Nyssa fissilis*, natural size, from Brandon lignite, showing great variation in shape and dimensions.

PLATE IV

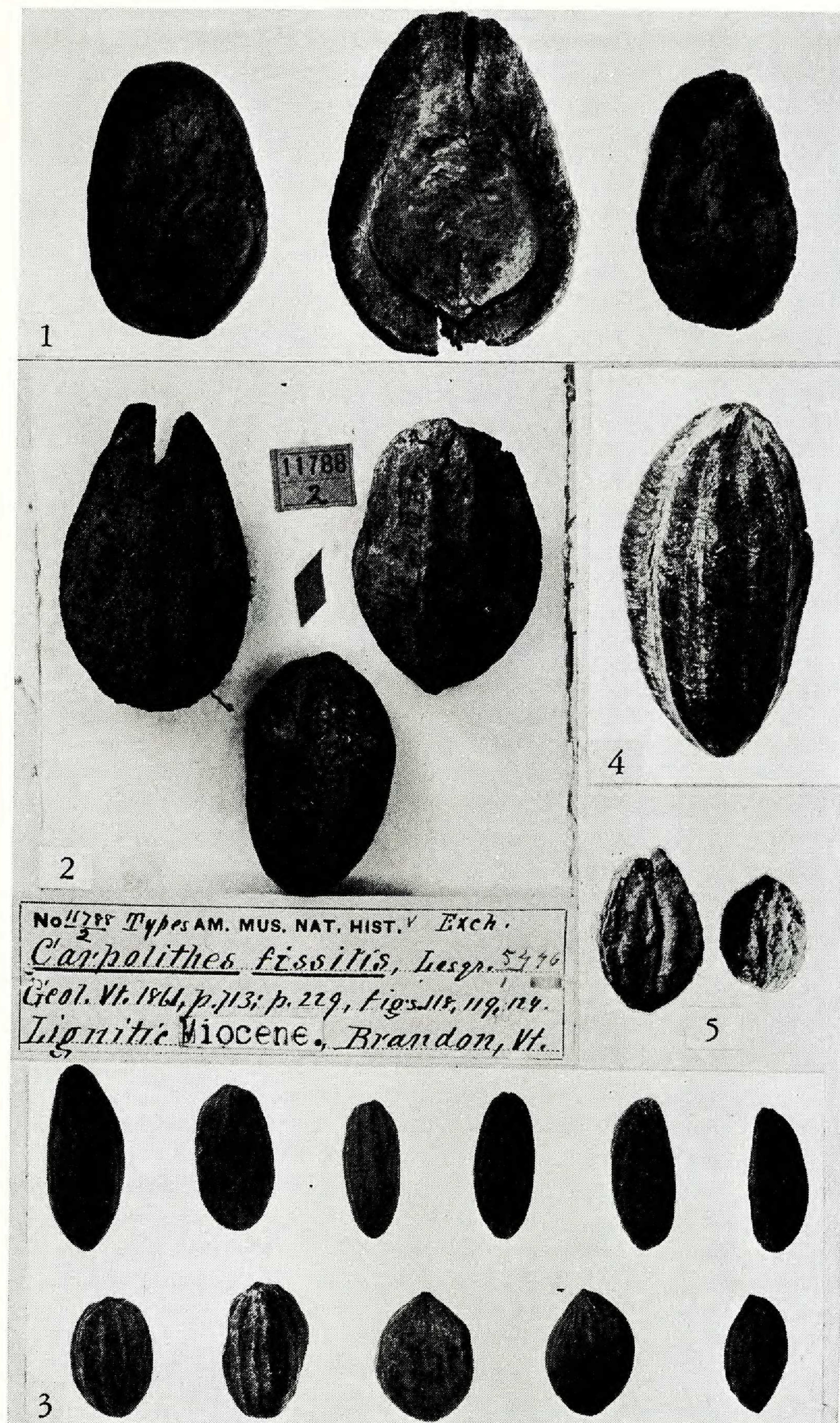
FIG. 14. Transections of bilocular *Nyssa fissilis*, $\times 5$, from Brandon, showing thickness and fibrous composition of endocarp wall — note remains of seed in upper section.

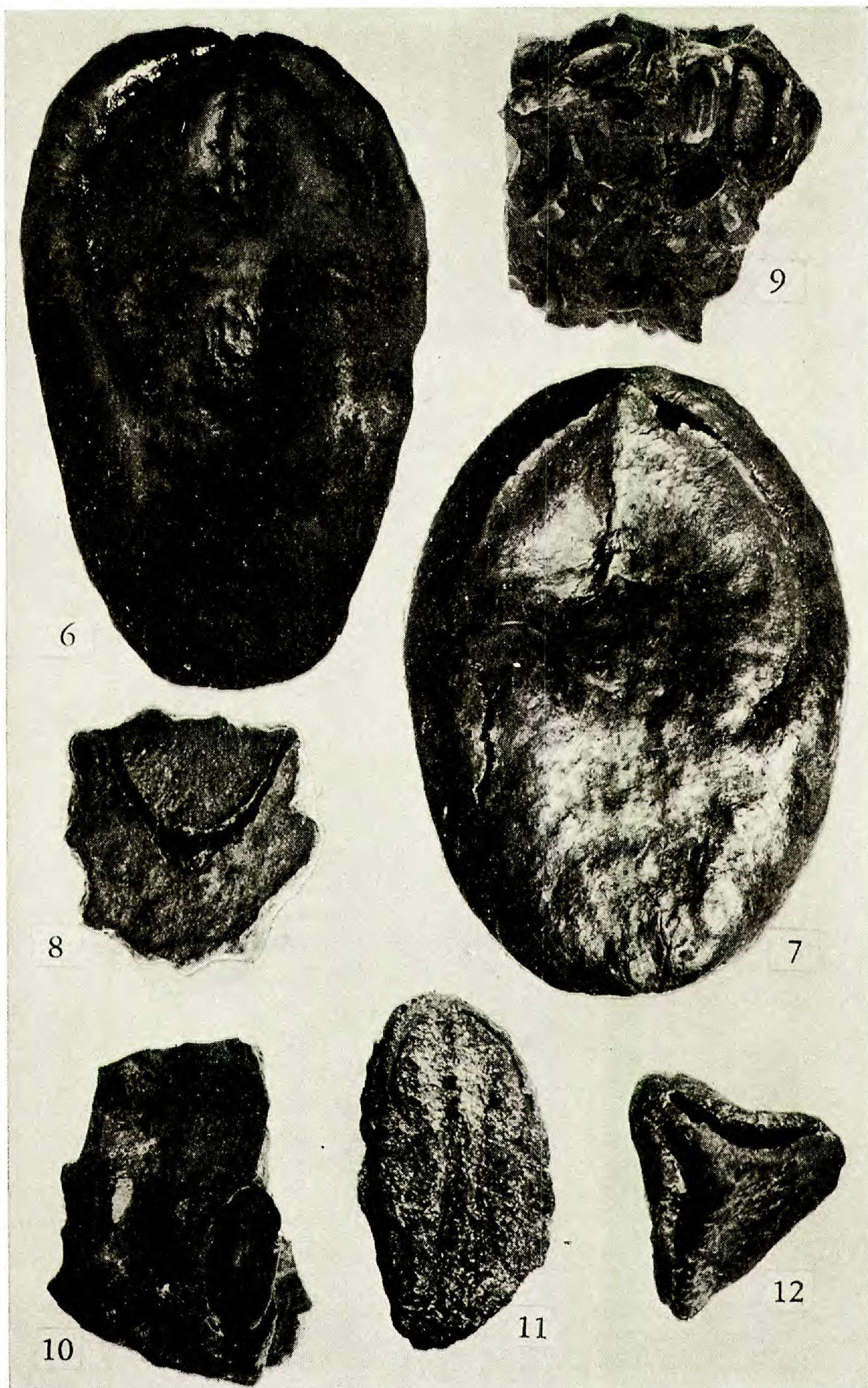
PLATE V

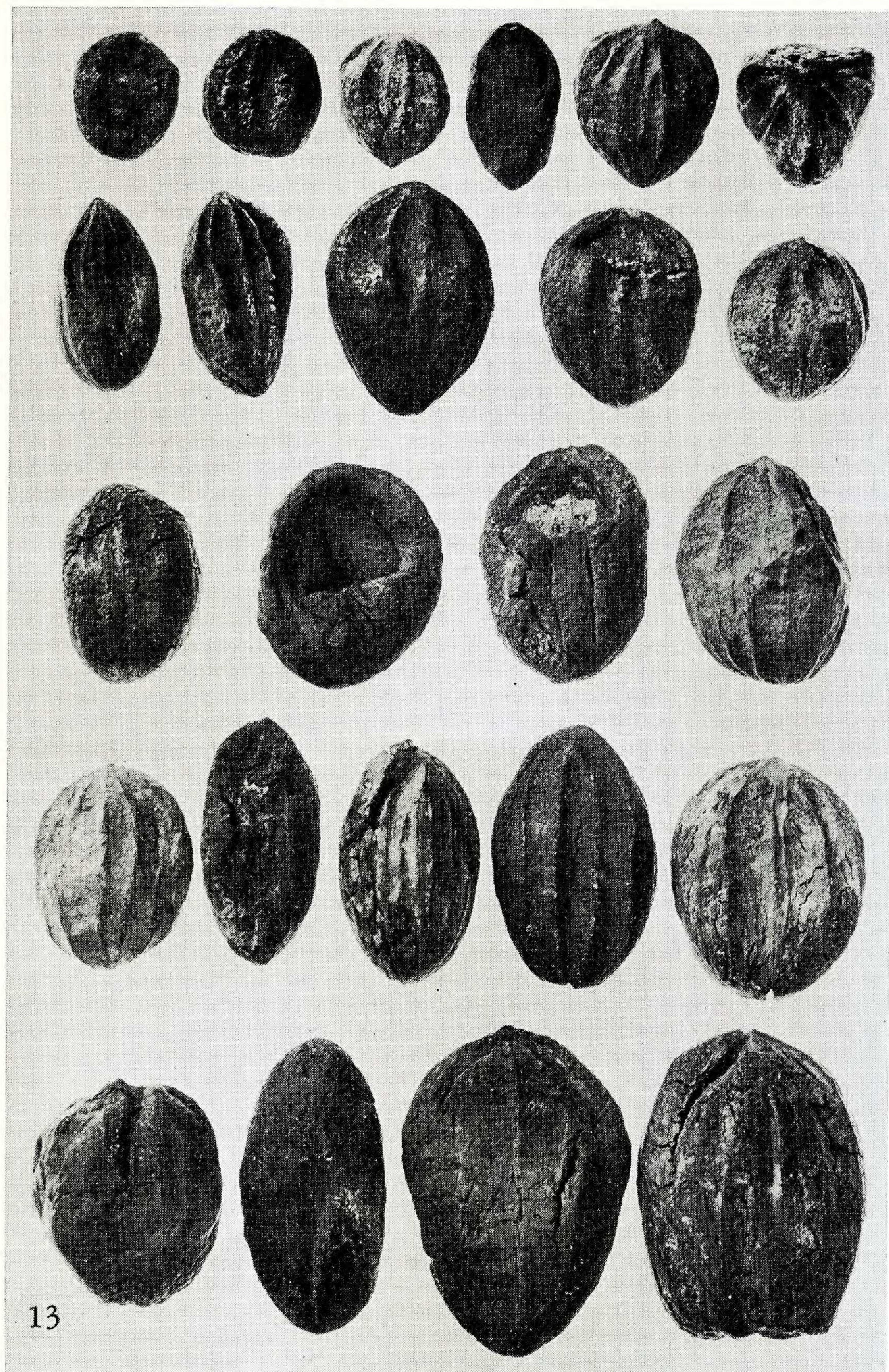
Figs. 15–19. *Nyssa complanata*, Brandon lignite. FIGS. 15 & 16, $\times 2.6$, show variation in size; fossils in FIG. 16 were photographed under water — note that peripheral bundles are more numerous in specimens on right than in modern *N. sylvatica*. FIGS. 17–19. Transections, $\times 10$. FIG. 17 is from a four-locular stone with a five-sided appearance owing to splitting along mid-dorsal line opposite one of the locules — note rupture and displacement of septa. FIGS. 18 & 19 show basal sections of two trilocular stones; individual carpels are recognizable here.

PLATE VI

FIGS. 20-28. FIG. 20. Oligocene fruit (half mold), $\times 2$, from Karnes Co., Tex., which resembles *Nyssa lescurii* in size and shape. FIG. 21. Eocene stone, $\times 2$, from Smithville, Tex., with similar features. FIG. 22. *The same*—opposite side. FIGS. 23-25. *N. fissilis* collected from Brandon silt (Paleobotanical Collections, Bot. Mus., Harvard No. 56601); these stones have undergone more intensive compression than the lignite specimens shown in FIG. 13. FIG. 23. Smallest example of *N. fissilis* known, $\times 2.8$. FIG. 24. *The same*, apical view. FIG. 25. Another stone, $\times 3$ —note prominence of dorsal ridges, narrow valve. FIG. 26. *N. pachycarpa*, $\times 2.7$; Japanese Pliocene. FIG. 27. *N. lescurii*, apical end $\times 5$, showing conical disk and rim along which perianth lobes were located. FIG. 28. *N. lescurii*, transection $\times 10$; both from Brandon.

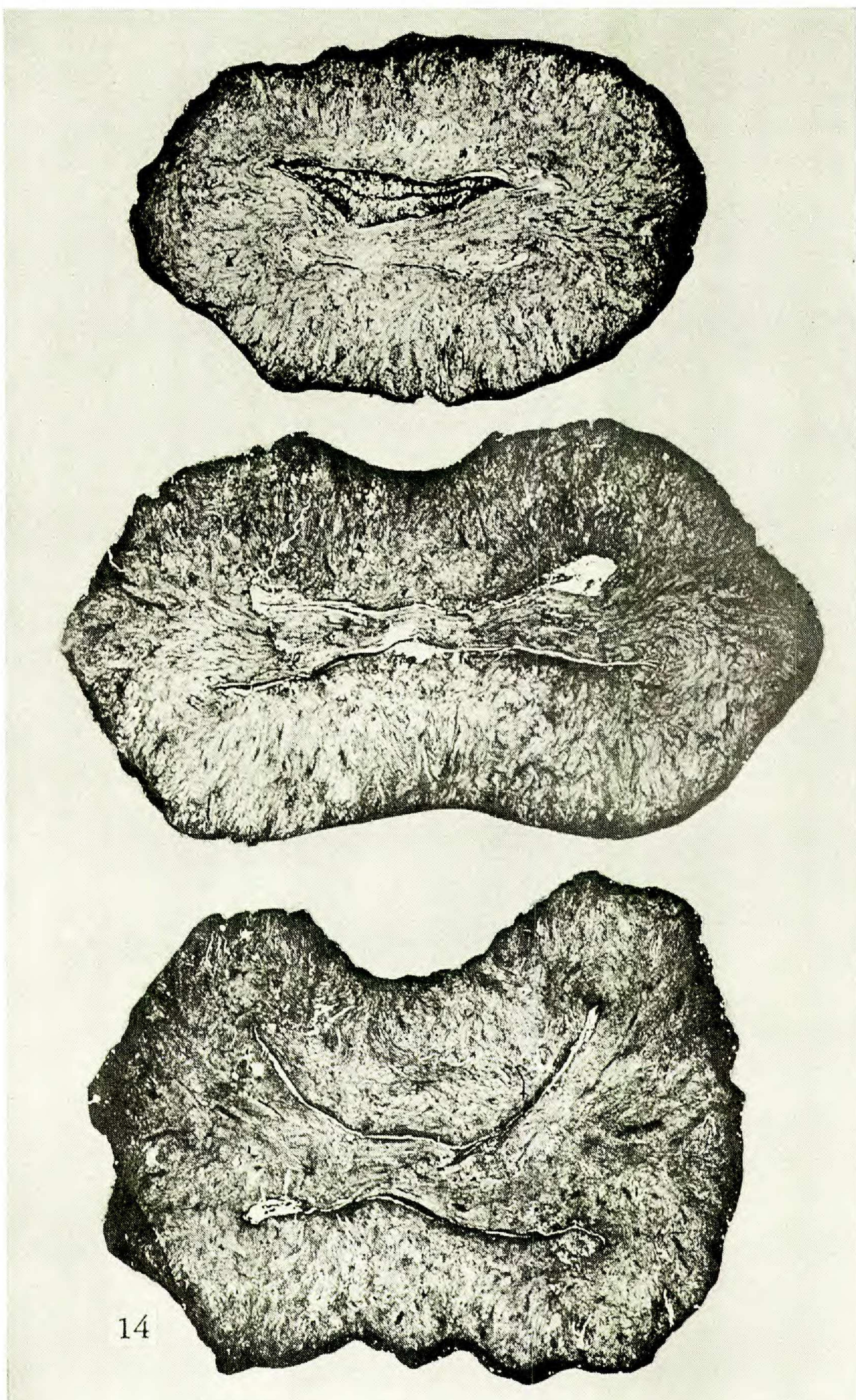






13

EYDE & BARGHOORN, STUDIES OF NYSSACEAE, II



14

EYDE & BARGHOORN, STUDIES OF NYSSACEAE, II

